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THE ROLE OF PHOSPHORUS AND NITROGEN IN REGULATING THE GROWTH OF ROOTED MACROPHYTES IN PRAIRIE RIVERS

by

GENEVIÈVE MARGARET CARR ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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Dedicated with love to my grandmother,
Florence Areson Carr

ABSTRACT

The aim of this research was to quantify the relationship between macrophyte biomass and concentrations of phosphorus (P) and nitrogen (N) in freshwater ecosystems. A literature survey revealed that approximately 30 % of the variability in macrophyte biomass in lakes and rivers worldwide is explained by a form of both P and N in the open water and the type of waterbody (river or lake). Macrophyte growth in the South Saskatchewan River, Saskatchewan, was enhanced downstream of the Saskatoon sewage treatment plant, however P and N concentrations explained only a portion of the variability in biomass. Artificial stream experiments demonstrated that macrophyte growth is greatest when sediment P concentrations are above 200 μg/g exchangeable P, corresponding to the observation that maximum biomass *in situ* is reached at approximately 200 μg/g sediment P. It is difficult to predict macrophyte abundance based on open-water and sediment P and N concentrations and management strategies designed to regulate macrophyte growth should integrate reductions in nutrient-loading with manual plant harvesting when abundance reaches undesirable levels.

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Chapter 1: Background to study

1.0 INTRODUCTION

The use of lakes and rivers as receiving waters for wastes from human activities (such as agricultural runoff and industrial and municipal effluent) has increased loading of nutrients, especially phosphorus (P) and nitrogen (N), to freshwater ecosystems and resulted in accelerated rates of eutrophication (Wetzel 1983). Research conducted over the last half century has found that these culturally-enriched systems usually have high rates of primary and secondary production, low species diversity, and community assemblages that are often considered undesirable, when compared to undisturbed bodies of water (Wetzel 1983; Hooper 1969).

The relationship between nutrients in freshwater and phytoplankton production in lakes has been clearly demonstrated, both within individual lakes and over a broad geographic range. For example, Schindler (1974) demonstrated through whole-lake experiments that phytoplankton production increased when nutrients, especially P, were added to oligotrophic lakes in northwestern Ontario. On a broader geographic scale, phytoplankton biomass was directly related to open-water total P concentrations for lakes across North America (Dillon and Rigler 1974). Phytoplankton biomass in the Rideau River, Ontario, is related to both open-water P and N concentrations (Basu and Pick 1995). In contrast to the clear relationship between nutrients and phytoplankton, the link between biomass of periphyton, or attached algae, and P and N concentrations in lakes and rivers is less distinct, possibly because periphyton biomass is more heavily influenced by physical and biotic factors than water chemistry (Cattaneo 1987; Horner and Welch 1981; Bothwell 1985). For rooted macrophytes, the relationship is even less clear, despite reports documenting changes in macrophyte species composition and productivity in response to increased nutrient loading (Kullberg 1974; Litav and Agami 1976; Chambers *et al.* 1991). The fact that rooted aquatic plants incorporate P and N from both the open-water and from bottom sediments (Carignan and Kalff 1980; Chambers *et al.*

1989; Barko *et al.* 1986) may explain the limited success in quantifying the impact of nutrient enrichment on macrophytes.

The aim of the research presented here was to investigate the relationship between macrophyte growth and open-water and sediment P and N concentrations in rivers, with specific emphasis on the South Saskatchewan River in the Canadian prairies. This introductory chapter reviews published literature regarding P and N dynamics in river ecosystems and how changes in nutrient loading to rivers affect the growth of submerged aquatic plants. Because of the paucity of information on macrophytes in lotic ecosystems, conclusions will also be drawn from our understanding of the ecology of aquatic plants in lakes. In addition, this chapter will outline the major goals and approaches of the subsequent research projects.

1.1 PHOSPHORUS AND NITROGEN IN RIVER ECOSYSTEMS

The importance of P and N in mediating biological processes in both terrestrial and aquatic systems has long been recognized. These nutrients are among the primary elements that limit the growth and productivity of terrestrial (Bates 1971) and aquatic (Gunnison and Barko 1989) plants and increases in P and N concentrations have been linked to increases in the productivity of both lakes (*e.g.* Schindler 1974; Edmonson and Lehman 1981; Aldridge *et al.* 1993) and rivers (Hynes 1969; Chambers *et al.* 1989). While it is now clear that P concentrations play a critical role in regulating the productivity of freshwater aquatic systems (Schindler 1974; Edmonson and Lehman 1981; Hynes 1970), the impact of N is less well defined. Howarth (1988) suggested that N is more important than P in regulating primary production in marine systems and recent investigations into the nutrient dynamics of lotic freshwater systems suggest that N can limit primary production when P is present in a system in excess (*e.g.* Grimm *et al.* 1981; Nichols and Keeney 1976*a*; Keeney 1973). This section will review the different forms and dynamics of P and N in aquatic systems, with specific reference to rivers.

1.1.1 Forms of phosphorus in aquatic systems

The majority of our current understanding of the behaviour of P in aquatic systems arises from the work of early researchers who focused on discriminating between the different forms of P in water (Rigler 1956, 1964; Coffin *et al.* 1949; Hutchinson and Bowen 1950; Hayes *et al.* 1952) and sediments (Mortimer 1941, 1942). P is present in natural waters primarily as phosphates that can be separated into orthophosphates, condensed phosphates and organically bound phosphates (APHA 1971; Olsen 1967). These can be dissolved in the water or bound to detrital material and cellular components of living organisms (APHA 1971). Inorganic P, as orthophosphate (PO_4^{3-}), is biologically available to primary producers for incorporation into their tissues (Lean 1973).

P in bottom sediments can play a major role in the P dynamics of lakes and rivers (Mortimer 1941, 1942; Syers *et al.* 1973; Enell and Löfgren 1988). Concentrations of P in sediments, mostly inorganic, are generally much higher than open-water concentrations (Syers *et al.* 1973). Phosphates can be present in sediments as dissolved ions in the interstitial water or adsorbed to sediment and organic particles (APHA 1971).

There has been considerable confusion over how to fractionate and analyse the different forms of P in water and sediments and concentrations reported prior to 1960 are inconsistent with respect to the form of P analysed (Olsen 1967). Analytical methods for P determination in open water focus on three pools: (1) total P, which is a measure of all forms of P in a sample of water, (2) total dissolved P, which is all dissolved forms of P, and (3) soluble reactive P, which consists largely of orthophosphate and also some condensed phosphates, and is an indicator of bioavailable P (APHA 1971). Analysis of sediment P can be divided into: (1) total P, which is the combined porewater and sediment-bound P, (2) porewater P, and (3) exchangeable P, which is the P adsorbed to sediment particles that can diffuse into the porewater as the latter becomes depleted (Enell and Löfgren 1988).

1.1.2 Forms of nitrogen in aquatic systems

Nitrogen (N) occurs in freshwater in a variety of inorganic and organic forms. Dissolved molecular N (N_2), ammonium (NH_4^+), nitrite (NO_2^-) and nitrate (NO_3^-) compose the inorganic pool (Wetzel 1983). Organic N is present as amino and amide N, as well as heterocyclic compounds such as purines and pyrimidines (Brezonik 1972). N compounds can be dissolved in water as soluble organic forms or inorganic ions, or they can be present as cellular constituents and nonliving particulate matter (Brezonik 1972; Keeney 1973). The concentration of the various forms of N in water are primarily mediated by biological activity (Brezonik 1972). Primary producers assimilate N as NH_4^+ and NO_3^-, and N is returned to the inorganic nutrient pool through bacterial decomposition and excretion of NH_4^+ and amino acids by living organisms (Brezonik 1972). Aerobic bacteria convert NH_4^+ to relatively stable NO_3^- and NO_2^- through nitrification, and anaerobic and facultative bacteria convert NO_3^- and NO_2^- to N_2 gas, through denitrification (Brezonik 1972). N-fixation, performed by blue-green algae and certain bacteria, converts dissolved molecular N_2 to NH_4^+ primarily when other N pools have been depleted in the water (Brezonik 1972).

N in bottom sediments is primarily organic, with some inorganic N present as NH_4^+ (Keeney 1973). Because sediments are generally anoxic, NO_3^- and NO_2^- concentrations tend to be low and NH_4^+ concentrations are usually high relative to the overlying water (Keeney 1973). N is present in sediments in the porewater, as dissolved N, or adsorbed to sediment and organic particles (Wetzel 1983).

There are many methods available to analyse for N in water and sediment samples. In general, interstitial and open-water samples are analysed for $NO_3^- + NO_2^-$ and NH_4^+ concentrations, to determine bioavailable or inorganic N (APHA 1971). Total Kjeldahl N measures NH_4^+ plus organic N and when added to $NO_3^- + NO_2^-$, gives a measure of total N in the water (APHA 1971). Total N is also determined from analyses of particulate plus dissolved N (APHA 1971). Sediment samples are usually analysed for exchangeable N, which reflects bioavailable N, and total N, which estimates organic N when the exchangeable fraction is removed (APHA 1971).

1.1.3 Nutrient spiralling in rivers

The P and N dynamics of lakes have typically been described in terms of circular cycles (Hutchinson 1948), with nutrients moving between lake sediments and the water column, the hypolimnion and epilimnion, and seasonally. However, circular systems are less easily discerned in rivers, because substances are continually displaced downstream (Hynes 1970; Webster and Patten 1979). While nutrients cycle in rivers both seasonally and between sediments and open water, their cycles are best described as spirals and not as circular causal systems (Webster and Patten 1979). Spiralling reflects the processes involved in cycling an element through its various phases while incorporating the downstream movement of the element (Wallace *et al.* 1977).

Periphyton and rooted plants in rivers incorporate dissolved P and N into their tissues, storing these nutrients until the plants are either consumed by other organisms or transported downstream as detrital matter (Wallace *et al.* 1977; Webster and Patten 1979). Organic matter can be trapped and consumed by filter feeders to meet their P and N requirements, or temporarily stored in sediments (Wallace *et al.* 1977). A spiral is completed when dissolved P and N that has been taken up by plants is released back to the water column through animal excretory products, death and bacterial decomposition of grazers and other organisms, and from the plants themselves (Wallace *et al.* 1977; Webster and Patten 1979). The length of a spiral is defined as the downstream distance required for an element to complete one entire cycle and is indicative of the efficiency of organisms within a stream to make use of the nutrients that flow past them (Elwood *et al.* 1981; Newbold *et al.* 1981). That is, when spiral length is short, nutrients are in high demand and organisms within the stream are considered highly efficient at processing the element, in comparison to streams with long spiral lengths where nutrients are in low demand (Wallace *et al.* 1977; Webster and Patten 1979; Elwood *et al.* 1981). Retention time in streams is the time it takes for the completion of a spiral and long retention times also indicate that nutrients are in high demand and are being stored within sediments and cellular components of organisms (Newbold *et al.* 1982).

Nutrient spiralling has been used as a measure of the resistance and resilience of a stream to perturbation (Webster and Patten 1979). Webster and Patten (1979) demonstrated that streams draining basins that had been perturbed by deforestation and replacement of natural stands of forest had longer spiral lengths and processed organic matter less efficiently than streams in drainage basins that had not been perturbed. Similarly, Chauvet and Décamps (1989) found that streams in deforested watersheds had longer spiral lengths with shorter retention times than streams draining undisturbed, mature forest ecosystems.

1.2 PHOSPHORUS AND NITROGEN AND THE GROWTH OF MACROPHYTES

As early as the 1920s, ecologists recognized the importance of nutrients and sediment type in regulating the abundance and distribution of macrophytes in lakes (Pearsall 1920, 1921; Spence 1967) and rivers (Butcher 1933; Westlake 1973). Concern over the rapid eutrophication of aquatic ecosystems has led to investigations into the responses of macrophytes to P and N enrichment and the mechanisms of P and N uptake by aquatic plants (*e.g.* Bristow and Whitcombe 1971; Toetz 1974; Carignan and Kalff 1980; Chambers *et al.* 1989). Most recently, researchers have approached the study of macrophytes from within a framework of ecosystem processes and attempted to determine how aquatic plants affect their surrounding environment (*e.g.* Gregg and Rose 1982; Carpenter and Lodge 1986; Sand-Jensen *et al.* 1989; Chambers and Prepas 1994).

1.2.1 Role of roots and shoots in nutrient uptake

Debate over the role of bottom sediments versus open water in supplying nutrients, primarily P and N, to aquatic plants has been ongoing since the 1920s (Denny 1980). Pearsall (1920, 1921) found no correlation between open-water nutrient concentrations and plant distribution in surveys of the English lakes, from which he concluded that macrophytes derive their nutrients from the sediments via their roots. However, Spence (1967) was unable to conclude with certainty that the distribution of macrophytes in Scottish lakes was determined by sediment nutrient content. Others, identified by Denny (1980), have assumed that because aquatic plants have small root systems, reduced conducting tissue, and thin leaves and cuticles, nutrient absorption must be through the leaves and shoots.

Experimental evidence from the last three decades has led to the general conclusion that rooted aquatic plants growing in lakes and rivers derive the majority of their required P from bottom sediments (Haslam 1978; Barko *et al.* 1991). Bristow and Whitcombe (1971), used ^{32}P to trace translocation of P in plants and found that 90, 59, and 74% of the P in the shoots of *Myriophyllum brasiliense*, *Myriophyllum spicatum* and *Elodea densa*, respectively, was derived from the roots. Bole and Allan (1978) also found that P was primarily incorporated through the roots of *Hydrilla verticillata* and *M. spicatum*, but that the relative amount of root absorption decreased with increasing concentrations of orthophosphate in the open water. Carignan and Kalff (1980) demonstrated *in situ* that nine species of rooted aquatic plants incorporated greater than 91 % of their P from the sediments in mesotrophic to mildly eutrophic waters, with shoots incorporating small amounts of P (approximately 29%) only under highly eutrophic conditions. Chambers *et al.* (1989) established that macrophyte biomass and shoot density in rivers in the Canadian prairies was largely determined by sediment chemistry, indicating that roots are the primary source of nutrient uptake for aquatic plants in lotic environments. Many others (DeMarte and Hartman 1974; McRoy and Barsdate 1970; Best and Mantai 1978;

Barko and Smart 1980, 1981; Moeller *et al.* 1988) have also demonstrated that roots of submerged macrophytes are capable of P incorporation in controlled laboratory conditions and *in situ*.

Lake and river sediments have also been demonstrated to be the primary source of N for aquatic plants (Barko *et al.* 1991). Using $^{15}NH_4^+$, Toetz (1974) found that under laboratory conditions two species of aquatic plants (*E. densa* and *Scirpus* sp.) incorporated NH_4^+ through their roots. Nichols and Keeney (1976*b*) used ^{15}N to trace the uptake and translocation of N in *M. spicatum* in the laboratory and determined that while uptake of N through roots was possible, it was preferentially incorporated via plant leaves. Barko and Smart (1981) found that four species of submerged macrophytes, grown in controlled environment chambers, mobilized N from sediments when the overlying water was N-deficient. Field surveys of Lake Wingra, Wisconsin, also demonstrated that tissue N levels of *M. spicatum* were correlated with sediment N levels, indicating that sediments are a significant source of N to rooted macrophytes (Nichols and Keeney 1976*a*). Results from *in situ* experiments performed by Rattray *et al.* (1991) supported previous findings that submerged macrophytes incorporate N through their roots when the overlying water is low in available N. Chambers *et al.* (1989) found that the aquatic macrophyte, *Potamogeton crispus*, mobilized much of its required N from bottom sediments when grown in flowing waters. Because sediments tend to be anoxic and therefore have high NH_4^+ concentrations relative to the overlying water (Keeney 1973), the ability of plants to mobilize NH_4^+ through their roots allows them access to an otherwise unavailable source of N (Toetz 1974).

1.2.2 Sediment type and phosphorus and nitrogen availability

Closely linked to the ability of aquatic plants to incorporate P and N through their roots are sediment type and nutrient availability (Barko *et al.* 1991). Observations of the distribution of aquatic plants in lakes and rivers have suggested that biomass and shoot density are also related to physical characteristics of the sediment, such as texture and bulk density (Pearsall 1920; Butcher 1933; Sculthorpe 1967; Bristow 1975; Haslam 1978). Sediment texture can affect a species' ability to penetrate the sediment surface and form roots (Bristow 1975; Denny 1980). Fine-textured sediments in lakes and rivers tend to have high porewater nutrient concentrations as a result of changes in sorption capacity, oxygen availability, microbial activity and groundwater intrusions (Chambers *et al.* 1992) that favour the colonization of rooted aquatic plants. Sediment nutrient availability is reduced by the presence of high concentrations of organic matter as P and N in solution become adsorbed to detrital particles (Barko *et al.* 1991). Decomposition and nutrient regeneration by microorganisms in sediments can stimulate macrophyte growth by making nutrients such as P and N available to plant roots for uptake (Gunnison and Barko 1989). However, these organisms can also inhibit plant growth by releasing phytotoxic compounds during the anaerobic decay of organic matter (Gunnison and Barko 1989). Boeger (1992) found that substratum influenced the growth of *Ranunculus aquatilis* in flowing water such that highest plant biomass was observed in fine-textured, nutrient-rich sediments, as compared to sand or gravel that typically had low nutrient concentrations. Barko and Smart (1986) surveyed 40 sediments from 17 North American lakes and also observed that macrophyte growth (*M. spicatum* and *H. verticillata*) was highly related to sediment density and organic content, which reflected nutrient availability.

1.2.3 Critical phosphorus and nitrogen concentrations and nutrient limitation in rooted aquatic plants

Critical to the development of nutrient reduction guidelines to control biomass of aquatic macrophytes is an understanding of the relative amounts of P and N required to sustain growth. Gerloff and Krombholz (1966) related plant tissue P and N concentrations to biomass in laboratory cultures and identified critical concentrations that resulted in maximum biomass. Critical tissue P and N contents of *Vallisneria americana*, *Elodea occidentalis*, *Ceratophyllum demersum* and *Heteranthera dubia* were approximately 1.3

and 0.13% dry weight, respectively (Gerloff and Krombholz 1966). Sytsma and Anderson (1993), comparing tissue nutrients to plant yield, found that leaves and stems of *M. aquaticum* were deficient in P below 0.16 and 0.10% dry weight, respectively, and deficient in N below 1.35 and 0.38% dry weight, respectively. Others (Wong and Clark 1979; Schmitt and Adams 1981; Colman *et al.* 1987) have related tissue P content to rates of photosynthesis, measured as carbon uptake, to determine critical nutrient contents for aquatic plants. These experiments have, in general, yielded lower estimates of critical nutrient concentrations, perhaps because they reflect an immediate response of plants to changes in nutrient levels (i.e. photosynthetic rate) rather than an integrated response typical of the plant yield experiments (Colman *et al.* 1987). Because of biochemical and morphological similarities among aquatic angiosperms, considerable variation in critical tissue P and N concentrations across species is not expected (Gerloff and Krombholz 1966; Duarte 1992). Based on the assumption of standardized critical P and N concentrations, *in situ* experiments could be designed to determine if and when plant growth is limited by nutrient availability.

Increases in plant biomass and rates of photosynthesis in response to added N or P can be used as indicators of nutrient limitation *in situ* (Howarth 1988). Anderson and Kalff (1986) demonstrated that biomass of *M. spicatum* in Lake Memphramagog increased significantly in response to sediment N enrichment, but not to P enrichment, suggesting that the plants were N-limited. Granéli (1985) fertilized water in reed stands in two Swedish lakes and found that *Phragmites australis* was also primarily N-limited. P in sediments was the limiting nutrient in an estuarine population of *Zostera marina* (Murray *et al.* 1992). Nichols and Keeney (1976*a*) reported that tissue N concentrations of *M. spicatum* in Lake Wingra were significantly correlated with available sediment N, which varied between sites and seasonally, suggesting that the degree of nutrient-deficiency depended on local conditions. In a survey of Wisconsin lakes, plant tissue contents were never below critical levels but relative amounts of P and N in tissues suggested that P would limit growth if nutrient supplies were depleted (Gerloff and Krombholz 1966).

While little work has been done on plant nutrient limitation in streams, Wong and Clark (1976) found that P concentrations in streams in southern Ontario were directly related to tissue P, but not N, content of the alga, *Cladophora*, which indicated that P limited the growth of this species. However, *Cladophora* was found to be primarily N-limited in the Clark Fork of the Columbia River, Montana based on tissue nutrient concentrations and nutrient uptake rates (Lohman and Priscu 1992).

1.2.4 Effects of macrophytes on phosphorus and nitrogen dynamics in lotic ecosystems

Research into the growth of submersed macrophytes in rivers has primarily focused on how the environment affects plant biomass, distribution and abundance, as opposed to how macrophytes influence the stream environment. However, studies during the past ten years provide increasing evidence that aquatic macrophytes modify the stream environment. Carpenter and Lodge (1986) suggest that aquatic plants represent an important link between biological communities in rivers, between river sediments and open water, and between aquatic and terrestrial systems. They alter the physical and chemical characteristics of their surroundings and in so doing can impact the nutrient dynamics of rivers (Barko *et al.* 1991; Chambers and Prepas 1994). Dense macrophyte beds cause reductions in flow rates and increase rates of deposition of nutrient-rich silt and organic matter (Butcher 1933; Gregg and Rose 1982; Carpenter 1981; Sand-Jensen *et al.* 1989). While macrophyte beds act as sinks for nutrients by trapping particulates, they also deplete sediment nutrient pools by incorporating porewater nutrients into their tissues through their roots (Carignan 1985; Jaynes and Carpenter 1986). Macrophytes in temperate regions store nutrients in their tissues on an annual cycle, which affects the retention time of P and N in aquatic systems (Carpenter and Lodge 1986). Decaying plant tissues release P and N to the water and become an important source of nutrients to aquatic organisms living in the water column (Carpenter 1981). Thus, while rooted aquatic plants are easily affected by changes in their environment, they can also markedly influence the physical, chemical and biological characteristics around them.

1.3 SUMMARY AND RESEARCH OBJECTIVES

To date, the relationship between the growth of rooted macrophytes and concentrations of P and N in rivers has been poorly quantified. While there is some evidence that suggests that growth of rooted aquatic plants is related to nutrients in lotic systems (*e.g.* Wright and McDonnell 1986; Carr and Goulder 1990), there is also conflicting evidence that finds no relationship between macrophytes and nutrient concentrations (*e.g.* Kern-Hansen and Dawson 1978; Canfield and Hoyer 1988). These contradictory reports may be the result of different approaches to studying nutrient limitation (such as *in situ* versus laboratory experiments, and monitoring changes in photosynthetic rate versus changes in either biomass or tissue nutrients) and highlight the need for a comprehensive study of the role of open-water and sediment-bound nutrients in regulating aquatic plant biomass in running waters. Without such a study, attempts to manage luxuriant plant growth in rivers will be ineffective, because they will not address the factors most likely to limit aquatic plant growth. Thus, the overall goal of this research was to quantify the relationship between macrophyte abundance and nutrient concentrations in the open-water and in the sediments in freshwater systems, particularly running waters. To address this objective, two research projects were undertaken.

Project 1 (Chapter 2): Modelling freshwater macrophyte biomass in relation to open-water phosphorus and nitrogen concentrations

The objective of this project was to quantify with multiple regression analyses the relationship between macrophyte biomass and open-water nutrient concentrations in lakes and rivers throughout the world, based on data collected in a detailed survey of published literature. This study assesses the predictability of rooted aquatic plant biomass based on open-water P and N concentrations, and makes comparisons to other empirical models generated for phytoplankton and periphyton communities in lakes and rivers over broad geographic ranges.

Project 2 (Chapter 3): Relationship between macrophyte growth and sediment phosphorus and nitrogen concentrations in the South Saskatchewan River, SK

The purpose of this project was to quantify the role of sediment nutrients in regulating macrophyte biomass in the South Saskatchewan River, SK, downstream of the City of Saskatoon's sewage treatment plant. Results from *in situ* observations and artificial stream experiments were used to assess the effectiveness of management strategies aimed at reducing aquatic plant biomass through nutrient reductions.

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Chapter 2: Modelling freshwater macrophyte biomass in relation to open-water phosphorus and nitrogen concentrations

2.0 INTRODUCTION

The ability of empirical models to predict patterns across a broad range of aquatic ecosystems has been demonstrated repeatedly over the past three decades (*e.g.* Dillon and Rigler 1974; Watson and Kalff 1981; Chambers and Kalff 1985; Canfield and Hodgson 1983). Earliest models were relatively simple input-output models used to predict total phosphorus (P) concentrations in lakes (Vollenweider 1975), and regression models to predict chlorophyll *a* concentrations from in-lake TP concentrations (Dillon and Rigler 1974). Empirical modelling has expanded more recently to examine multivariate relationships between nutrients and biomass of benthos (Hanson and Peters 1984), zooplankton biomass (Pace 1986), fish yield (Hanson and Leggett 1982), and periphyton biomass in lakes (Cattaneo 1987). These models have become important tools in nutrient and fisheries management in lakes and led to the formulation of limnological theories that could then be tested through observation and experimentation (Peters 1986).

The aim of this study was to develop an empirical model relating open-water P and nitrogen (N) concentrations to macrophyte biomass in lakes and rivers. Rooted macrophytes are a critical component of aquatic ecosystems (Wetzel and Hough 1973; Wetzel 1983) but the response of aquatic plants to P and N enrichment has not been clearly quantified. Studies into the relationship between macrophyte growth and P and N have yielded contradictory results. For example, Smith *et al.* (1978) documented high aquatic plant biomass downstream of a fish processing plant in the Crnojevića River, Yugoslavia, but found no relationship between macrophyte growth and concentrations of P in the water. Similarly, macrophytes were abundant in the South Saskatchewan River, SK, downstream of the City of Saskatoon's sewage treatment plant, but the region of peak biomass in the river did not correspond to the region of peak P and N concentrations (Chapter 3). In contrast, Carbiener *et al.* (1990) found that aquatic plant community composition was strongly correlated with ammonium and soluble reactive P concentrations in the Rhine River, France. The lack of clear and consistent correlations between macrophyte biomass and P and N concentrations has led to the hypothesis that since rooted macrophytes incorporate the majority of their P and N from bottom sediments (*e.g.* Chambers *et al.* 1989; Barko *et al.* 1991; Carignan and Kalff 1980; and many others), sediment P and N concentrations may be better predictors of plant biomass within specific bodies of water (Canfield and Hoyer 1988). However, only 30% of the variability in macrophyte biomass in the South Saskatchewan River was explained by sediment P concentrations (Chapter 3) and a survey of 19 Danish streams found no link between macrophyte biomass and sediment nutrient concentrations (Kern-Hansen and Dawson 1978). The conflicting evidence into the role of nutrients in regulating aquatic plant growth may be due to the scale at which these patterns are investigated. Duarte and Kalff (1990) proposed that factors that control macrophyte growth within an aquatic system may be different from those acting over a broader geographic range. Therefore, while P and N in sediments may be directly related to aquatic plant biomass in individual lakes and rivers, as suggested by Canfield and Hoyer (1988), open-water P and N concentrations may be better predictors of biomass over a broad geographic range.

This paper reviews data from the literature to test the utility of open-water P and N concentrations in predicting macrophyte biomass in lakes and rivers. Few studies have attempted to predict macrophyte abundance based on open-water nutrients and the results from these studies have been contradictory. For example, submerged macrophyte biomass was not related to open-water P and N concentrations for 25 lakes in Canada and the United States (Duarte and Kalff 1990), 19 streams in Denmark (Kern-Hansen and Dawson 1978), or 17 streams in Florida (Canfield and Hoyer 1988), although in the case of the Florida study, the lack or correlation was attributed to the fact that the streams were nutrient-saturated and therefore plant biomass was unlikely to be determined by nutrient concentrations. In contrast, Smith and Wallsten (1986) found using multiple regression analysis that total nitrogen (N), but not P, concentration in lake water was an important predictor of the percentage cover of emergent and floating-leaved macrophytes in Central Swedish lakes ($r^2 = 0.91$). In this study, data on mean and maximum macrophyte biomass and open-water P and N concentrations were compared for 81 rivers and 69 lakes located throughout the world.

2.1 METHODS

Data on mean and maximum submerged macrophyte biomass (g/m^2) and open-water P and N concentrations (μg/L) from lakes and rivers were compiled from the literature. Mean biomass (B_{mean}) was recorded either as the average of all sites within a waterbody for the period of peak biomass (usually late July through early September in the Northern Hemisphere), or as the average of peak biomass collected over several seasons. Maximum plant biomass (B_{max}), taken from the period of peak biomass, was recorded as the highest value of the observed range when presented, or as the mean biomass plus either two standard deviations or one 95% confidence interval. Biomass was recorded in units of oven-dry weight and, when other units were reported, biomass was converted to dry weight by assuming dry weight to be 10% of fresh weight (Westlake 1965), ash free dry weight to be 80% of dry weight, and total organic carbon to be 37% of dry weight (Westlake 1974). Open-water nutrients included total P (TP), total dissolved P (TDP), soluble reactive P (SRP), total N (TN), total Kjeldahl N (TKN), total inorganic N (TIN), ammonium (NH_4^+), and nitrate plus nitrite (NO_2+NO_3). When only nitrate was reported, it was used in place of NO_2+NO_3, since nitrite concentrations are generally low. When TKN and NO_2+NO_3 or total dissolved N and particulate N were reported, they were summed to represent TN. Similarly, when NH_4^+ and NO_2+NO_3 were reported, these values were added to determine TIN. When only SRP or TDP concentrations were reported, TP was predicted from these values based on linear regressions of the untransformed concentrations that were generated from the available data, explaining over 98% of the variation in TP ($TP = 34.4 + 1.10(SRP)$, $n = 21$, $r^2 = 0.98$; $TP = 34.9+0.97(TDP)$, $n = 12$, $r^2 > 0.99$). Similarly, TN concentrations were predicted from a linear relationship with NO_2+NO_3 that explained ≥ 91% of the variation in TN ($TN = 425 + 1.35(NO_2+NO_3)$, $n = 19$; $r^2 = 0.91$). When estimates of NO_2+NO_3 were not accompanied by NH_4^+ concentrations, TIN concentrations were predicted based on a linear relationship with NO_2+NO_3 that explained approximately 97% of the variation in TIN (TIN = 137 + 1.08(NO_2+NO_3), $n = 29$; $r^2 = 0.97$).

The relationship between mean and maximum macrophyte biomass and open-water nutrient concentrations was assessed using stepwise multiple regression for the entire dataset with rivers and lakes distinguished with a dummy variable (SPSS 1993). To ensure independence of observations, only one estimate of biomass and open-water nutrients was entered for each waterbody. Thus, when parameters for individual lakes or rivers were encountered in two or more published sources, the source that provided data for the most number of parameters was selected for the model. When equal biomass and nutrient parameters were reported in several sources for a waterbody, the source of the data was randomly selected. Mean and maximum biomass were square-root transformed to normalize their distribution about the independent variables. Independent variables were transformed when necessary to meet the regression assumption of linearity. Dependency among nutrient parameters was tested by examining the Pearson correlation coefficients, and subsets of variables that were not highly correlated were entered separately into multiple regression models.

2.2 RESULTS

The data set consisted of 81 rivers and 69 lakes from across the world. The majority of lakes were from Canada (45), the United States (12) and Europe (9), but data from two lakes in New Zealand and one in Africa were also included. The rivers included in the data set were from Canada (8), the United States (52) and Europe (21). The raw data used in this study are presented in Appendix A. Open-water nutrient concentrations ranged from oligotrophic to eutrophic for both lakes and rivers (Table 2.1). It was rare that all of the nutrient parameters investigated in this study were reported for one waterbody and, as a result, the number of observations decreased when multivariate

Table 2.1: Summary statistics (mean, minimum, maximum, and number of observations) of all parameters collected, for lakes and rivers.

Variable	Mean	Minimum	Maximum	No. of observations
Lakes				
Mean biomass (g/m^2)	142	0.1	801	68
Maximum biomass (g/m^2)	314	0.3	1950	61
TP (μg/L)	45	3	571	65
TDP (μg/L)	40	1	117	9
SRP (μg/L)	62	1.4	490	11
TN (μg/L)	662	83	1704	32
TKN (μg/L)	554	180	1100	8
TIN (μg/L)	256	12	1163	23
NH_4	123	3	540	22
$NO_2 + NO_3$ (μg/L)	125	4	950	24
Rivers				
Mean biomass (g/m^2)	386	1	34	81
Maximum biomass (g/m^2)	585	2060	3500	60
TP (μg/L)	193	36	1950	81
TDP (μg/L)	272	7	1350	7
SRP (μg/L)	127	2	1150	41
TN (μg/L)	3254	20	48513	68
TKN (μg/L)	702	99	2670	21
TIN (μg/L)	3458	14	38693	45
NH_4	294	6	1840	11
$NO_2 + NO_3$ (μg/L)	3927	6.4	35700	34

models were attempted. TDP was seldom reported in the literature and consequently its effect on macrophyte biomass was excluded from multivariate analyses. TKN and NH_4^+ concentrations were also excluded from multivariate models because they could not be transformed to meet the regression assumptions of linearity.

Open-water concentrations of P and N were significantly correlated with the type of waterbody and were consistently lower in lakes than in rivers (Table 2.2). All forms of both P and N were, in general, highly correlated and therefore only one form of each nutrient was entered into the models at a time (Table 2.2). P and N parameters were positively correlated with each other, indicating that areas with high P concentrations also tended to have high concentrations of N (Table 2.2).

There was no single nutrient parameter that was an ideal predictor of macrophyte biomass in lakes and rivers, however both mean and maximum biomass were best explained by the type of waterbody and a form of P and N (Table 2.3). SRP and TN along with the type of waterbody explained 30% of the variability in mean biomass, while maximum biomass was best explained ($r^2 = 0.33$) by the type of waterbody and the concentrations of TP and NO_2+NO_3 (Table 2.3; Figure 2.1). Biomass was positively correlated with concentrations of P, negatively correlated with concentrations N, and was higher in rivers than in lakes (Table 2.3).

2.3 DISCUSSION

Macrophyte biomass was significantly related to open-water P and N concentrations, but the predictive power of these relationships was low (Table 2.3). The type of waterbody (lake or river) and some form of P and N are the best predictors of biomass, with biomass increasing with increasing concentrations of P and decreasing concentrations of N (Table 2.3). Because P and N are positively correlated, it is likely that highest biomass occurs at intermediate concentrations of these nutrients and that high levels of N may have an

Table 2.2: Pearson correlation coefficients for variables used as predictors of macrophyte biomass in multiple regression models. Nutrient parameters transformed to meet assumptions of linearity. "R/L" is the waterbody type, with rivers and lakes coded as zero and one, respectively. All other abbreviations defined in text. Only significant (α = 0.05) coefficients presented.

	ln(TP)	ln(SRP)	ln(TN)	ln(TIN)	ln(NO_2+NO_3)	R/L
ln(TP)	–	0.94	0.51	0.50	0.41	-0.49
ln(SRP)		–	0.57	0.58	0.58	-0.41
ln(TN)			–	0.92	0.91	-0.30
ln(TIN)				–	0.93	-0.56
ln(NO_2+NO_3)					–	-0.70
R/L						–

Table 2.3: Regression models predicting mean and maximum macrophyte biomass (B_{mean} and B_{max}, respectively) in relation to open-water nutrient concentrations. "R/L" refers to type of waterbody and is coded zero for rivers and one for lakes. All other abbreviations defined in text.

Equation	r^2	*n*	*P*
$\sqrt{B_{mean}} = 32.72 - 6.47(R/L) + 2.78\ln(SRP) - 3.85\ln(TN)$	0.30	38	0.002
$\sqrt{B_{mean}} = 32.47 - 2.13\ln(TN) - 8.75(R/L)$	0.21	99	< 0.001
$\sqrt{B_{mean}} = 17.17 - 7.23(R/L)$	0.15	149	< 0.001
$\sqrt{B_{mean}} = 10.00 + 1.18\ln(SRP)$	0.09	51	0.020
$\sqrt{B_{max}} = 32.53 + 2.62\ln(TP) - 3.20\ln(NO_2+NO_3) - 13.71(R/L)$	0.33	50	< 0.001
$\sqrt{B_{max}} = 25.46 + 4.52\ln(TP) - 3.64\ln(TN)$	0.22	76	< 0.001
$\sqrt{B_{max}} = 7.37 + 2.76\ln(TP)$	0.12	121	< 0.001
$\sqrt{B_{max}} = 21.55 - 6.89(R/L)$	0.09	121	0.001

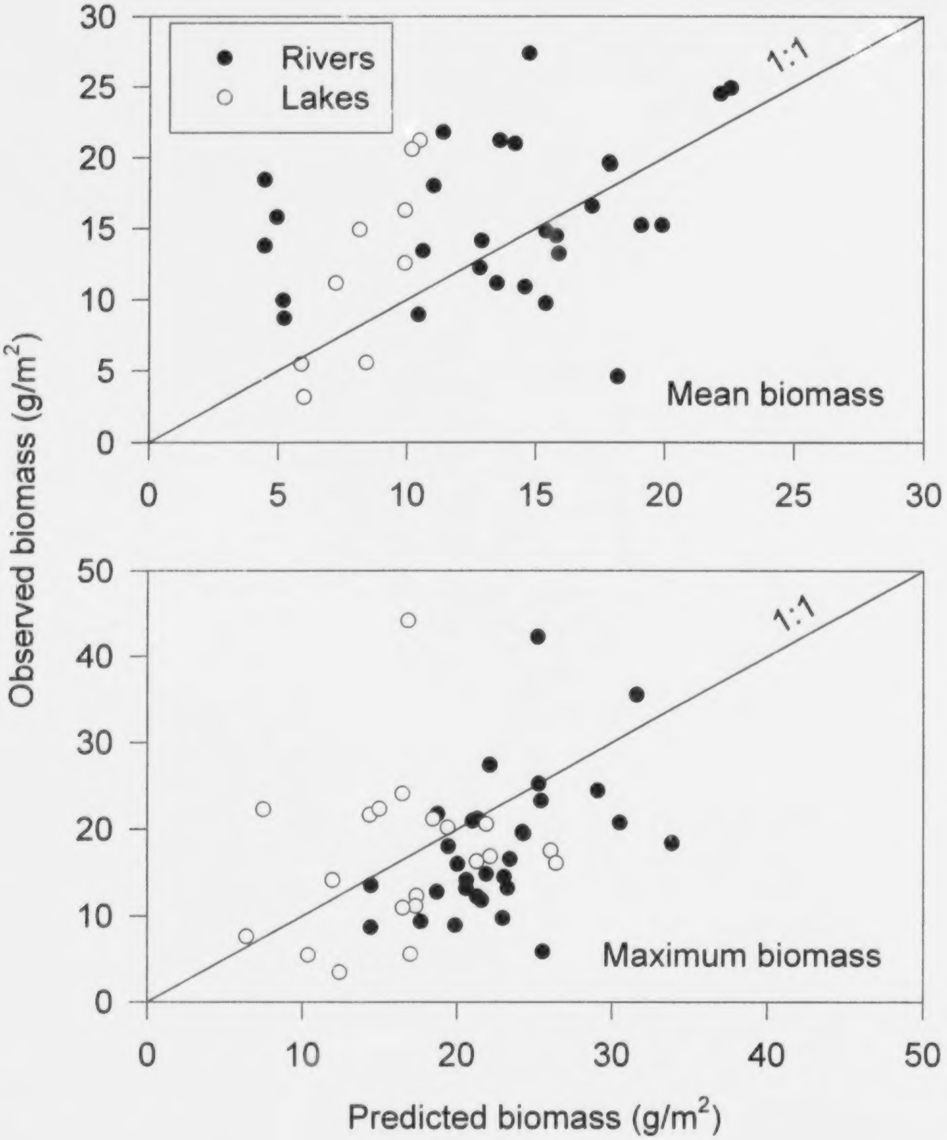

Figure 2.1: Relationship between mean and maximum observed and predicted biomass of aquatic macrophytes (square-root transformed) in lakes and rivers, based on multiple regression analyses. Mean biomass is predicted based on waterbody type (R/L), ln(SRP), and ln(TN), and maximum biomass is predicted based on waterbody type (R/L), ln(TP), and ln(NO_2+NO_3) (Table 2.3).

inhibitory effect on macrophyte growth. Carbiener *et al.* (1990) reported that ammonium toxicity was responsible for shifts in macrophyte community assemblages in streams on the Upper Rhine plain, France, and also that community associations were positively correlated with NH_4^+ and negatively correlated with SRP concentrations. The relationships observed globally in this study as well as those observed at an ecosystem level in that of Carbiener *et al.* (1990) highlight the importance of investigating the role of both P and N in regulating macrophyte biomass, because while either nutrient may give an indication of the trophic status of an ecosystem the combination of both nutrients will show any interaction between the plant and nutrient variables.

While this is the only study to have examined the role of P and N in regulating macrophyte biomass in both lakes and rivers on a global scale, empirical models developed for either lakes or rivers have found that macrophyte biomass can be predicted by factors in addition to P and N. For example, in a survey of 139 lakes from around the world, lake size and underwater light were good predictors of macrophyte biomass (Duarte *et al.*1986). Similarly, Duarte and Kalff (1990) surveyed 25 lakes from Canada and the United States and reported that lake-average submerged biomass could be predicted ($r^2 = 0.80$, $P < 0.0001$) by water alkalinity and littoral slope. Canfield and Duarte (1988) further stressed the importance of light availability and littoral slope in predicting macrophyte biomass in Florida lakes. Smith and Wallsten (1986) found that areal cover of emergent macrophytes in Central Swedish lakes could be predicted ($r^2 = 0.91$) from lake surface area, mean depth and open-water TN concentrations. Macrophyte biomass in Florida streams and spring-runs was not related to nutrient concentrations, but could be predicted ($r^2 > 0.93$ and $r^2 = 0.58$, respectively) by the degree of shading by riparian vegetation (Canfield and Hoyer 1988; Duarte and Canfield 1990). The study presented here is the only one to date that has investigated the role of P and N in regulating macrophyte biomass, irrespective of the type of waterbody.

This study found that open-water P and N concentrations in rivers and lakes explained no greater than 33% of the variability in macrophyte biomass (Table 2.3). P and N concentrations did not explain any significant variation in macrophyte biomass surveys for 17 Florida streams (Canfield and Hoyer 1988), 31 Florida spring-runs (Duarte and Canfield 1990), 19 Danish streams (Kern-Hansen and Dawson 1978), and 25 lakes from Quebec, New York and Vermont (Duarte and Kalff 1990). In contrast, open-water P and N concentrations are excellent predictors of phytoplankton biomass in lakes, with surveys of Florida, North American, and U.S. lakes finding that between 70 and 95% of the variability in phytoplankton biomass can be explained by P and N concentrations (Table 2.4). The relationship between concentrations of P and N and phytoplankton biomass was not, however, as strong in impoundments (r^2 = 0.38), an intermediate between lakes and rivers, or streams (r^2 = 0.53 for Missouri streams and r^2 = 0.16 for the Rideau River, Ontario) (Table 2.4). Furthermore, surveys of Quebec lakes, Antarctic lakes, and Danish streams found that periphyton biomass was not as well predicted (r^2 = 0.27 to 0.61) as lake phytoplankton biomass by open-water P and N concentrations (Table 2.4). This comparison of freshwater plant biomass responses to P and N concentrations suggests that as the complexity of aquatic plants increases from algae to rooted macrophytes, the predictability of plant biomass based solely on nutrient parameters decreases. Predictions of rooted macrophyte biomass based on open-water P and N concentrations are confounded because macrophytes can incorporate these nutrients from both the open-water and the sediments of lakes and rivers, and their biomass can be further influenced by factors particular to sediments, such as groundwater inputs, microbial activity, sediment fertility, pH, and redox conditions (Barko *et al.* 1991). Moreover, the poor predictability of both macrophyte and periphyton biomass, when compared to phytoplankton communities, may be due to high spatial heterogeneity in the physical environments in which these plants are found, resulting in patchy biomass distributions throughout a waterbody (Downing and Anderson 1985; Morin and Cattaneo 1992). Thus, as the complexity of aquatic plants increases, so do the number of factors that can

Table 2.4: Empirical models predicting biomass of aquatic plants (phytoplankton, periphyton, macrophytes) based on nutrient concentrations in aquatic ecosystems.

Waterbody	Plant type	Equation	r^2	n	P	Reference
North American lakes	Phytoplankton	$\log(\mathrm{chl}a) = 1.58\log(\mathrm{TP}) - 1.13$	0.95	56	< 0.001	Dillon & Rigler 1974
Florida lakes	Phytoplankton	$\log(\mathrm{chl}a) = -2.49 + 0.27\log(\mathrm{TP}) + 1.06\log(\mathrm{TN})$	0.81	223	< 0.05	Canfield 1983
U.S. lakes	Phytoplankton	$\log(\mathrm{chl}a) = 2.11 + 0.77\log(\mathrm{TP})$	0.71	149	< 0.05	Søballe & Kimmel 1987
U.S. impoundments	Phytoplankton	$\log(\mathrm{chl}a) = 1.79 + 0.60\log(\mathrm{TP})$	0.38	366	< 0.05	Søballe & Kimmel 1987
Missouri streams	Potamoplankton	$\log(\mathrm{chl}a) = 0.1 + 0.39\log(\mathrm{TP}) + 0.34\log(\mathrm{TN})$	0.53	36	< 0.05	Jones *et al.* 1984
Danish estuaries	Phytoplankton	$\mathrm{chl}a = 0.018(\mathrm{TN}) - 2.4$	0.61	20	< 0.001	Nielsen *et al.* 1989, *in* Sand-Jensen & Borum 1991
Rideau River, Ont.	Potamoplankton	$\log(\mathrm{chl}a) = 0.84\log(\mathrm{TP}) - 0.42$	0.16	36	0.016	Basu & Pick 1995
Quebec lakes	Periphyton (0.1 m)	$\mathrm{chl}a = 3.6(\mathrm{TP})^{0.61}$	0.30	13	n.s.	Cattaneo 1987
Quebec lakes	Periphyton (1.0 m)	$\mathrm{chl}a = 12(\mathrm{TP})^{0.42}$	0.27	13	n.s.	Cattaneo 1987
Antarctic lakes	Periphyton	$\mathrm{chl}a = 0.54 + 1.79(\text{porewater TP})$	0.34	12	< 0.02	Hansson 1992
Danish streams	Periphyton (max)	$\mathrm{chl}a = 929(\mathrm{SRP})/(49.2+\mathrm{SRP})$	0.61	21	< 0.001	Kjeldsen 1994
Lakes and rivers worldwide	Macrophytes (mean)	$\sqrt{B_{mean}} = 72.72 + 2.78\ln(\mathrm{SRP}) - 3.85\ln(\mathrm{TN}) - 6.47(R/L)$	0.30	38	0.002	This study
Lakes and rivers worldwide	Macrophytes (maximum)	$\sqrt{B_{max}} = 32.53 + 2.62\ln(\mathrm{TP}) - 3.20\ln(\mathrm{NO_2+NO_3}) - 13.71(R/L)$	0.33	50	< 0.001	This study

influence biomass accrual, making it difficult to predict biomass based solely on one or a few factors.

In addition to differences among aquatic plant groups in their response to nutrients, macrophyte biomass and nutrient concentrations were consistently higher in rivers than in lakes (Table 2.1). This pattern contradicts what was observed by Søballe and Kimmel (1987) for algae, namely that despite higher TP concentrations in rivers, algal abundance per unit P was lowest in rivers and highest in lakes, suggesting that abiotic factors override nutrients in limiting algal production in lotic ecosystems. Higher biomass of rooted macrophytes in rivers observed in this study, however, is most likely due to higher rates of photosynthesis resulting from the constant supply of dissolved nutrients and gases to plant shoots provided by flowing water (Madsen and Adams 1988; Westlake 1967). Moreover, higher nutrient concentrations in rivers may be because they are the dominant receivers of nutrient-rich wastes from agricultural, municipal and industrial activity. It is also possible that differences in macrophyte biomass between lakes and rivers are an artifact of the available data and reflect the general perception that macrophytes are a greater nuisance in rivers because they can impede boat traffic and increase the potential for flooding. In lakes, however, macrophytes are often perceived as less of a nuisance and more an integral part of the ecosystem, associated with clear water and low algal abundances (Barko *et al.* 1986; Wetzel and Hough 1973; Canfield *et al.* 1983). Thus, it may be that studies of macrophytes in lotic ecosystems are conducted in cases where biomass is high and potentially problematic, while studies in lentic ecosystems are conducted to further our understanding of macrophyte ecology. This study has demonstrated that macrophyte biomass in lakes and rivers is weakly related to open-water P and N concentrations. It is likely that the complexity of rooted macrophytes, when compared to algal communities, results in many factors influencing biomass that confound empirical models developed to predict biomass based on only one or a few factors.

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Chapter 3: Relationship between macrophyte growth and sediment phosphorus and nitrogen concentrations in the South Saskatchewan River, SK

3.0 INTRODUCTION

The impact of changes in phosphorus (P) and nitrogen (N) loading on the abundance and diversity of submerged plants in rivers has long been debated, particularly with respect to the effect of nutrient mitigation strategies in reducing excessive aquatic macrophyte production. For example, Wright and McDonnell (1986*a*, 1986*b*) predicted, on the basis of a model developed for Central Pennsylvania rivers, that reductions in open-water P concentrations would lower submerged plant biomass. In a laboratory study on the impacts of fish-farm effluents, Carr and Goulder (1990) demonstrated that inorganic P released from these effluents can increase growth of the macrophyte *Ranunculus penicillatus* in rivers in the United Kingdom. Similarly, Chambers *et al.* (1991) reported that biomass of rooted aquatic plants in rivers on the Canadian prairies can reach levels greater than 1000 g/m^2 downstream of municipal sewage outfalls compared to values of close to zero upstream of these nutrient-rich effluents. Declines in species diversity in rivers of Israel have also been associated with point-source loading of P and N (Litav and Agami 1976), while in the former Soviet Union, some riverine plant species have been found to be more resistant to nutrient-rich industrial and municipal wastes than others (Zeifert *et al.* 1991). In contrast, other researchers (*e.g.* Westlake 1973; Madsen and Adams 1988) have argued that aquatic plants are relatively insensitive to chemical inputs and that changes in macrophyte abundance and distribution are more likely a result of increased turbidity and the accumulation of organic matter downstream of point-source inputs. For example, Smith *et al.* (1978) reported abundant growth of submerged and floating-leaved macrophytes downstream of a fish processing plant in the Crnojevića River, Yugoslavia, but found no relationship between P and N in the river and macrophyte growth. Furthermore, studies of streams in Florida (Canfield and Hoyer 1988), the Holston River, Tennessee (Peltier and Welch 1969), and lowland streams in Denmark (Kern-Hansen and Dawson 1978) found no relationship between macrophyte growth and open-water P and N concentrations.

The aim of this study was to quantify the relationship between P and N and aquatic macrophyte growth in the South Saskatchewan River, SK, downstream of the City of Saskatoon's nutrient-rich municipal sewage outfall. Previous studies on macrophyte growth in response to nutrient enrichment focused for the most part only on open-water P and N concentrations. However, aquatic plants appear to incorporate the majority of their required P and N from bottom sediments rather than the water column in both rivers (Chambers *et al.* 1989) and lakes (Bristowe and Whitcombe 1971; Carignan and Kalff 1980; Barko *et al.* 1991). While the chemistry of bottom sediments is partially dependant on the chemistry of the overlying water (Chambers *et al.* 1992), sediment P and N concentrations are also determined by underlying geology, sediment particle size, and organic carbon concentrations (Meyer 1979; Hill 1982; Barko *et al.* 1991). P and N in groundwater inputs have also been shown to alter the chemistry of bottom sediments (Lodge *et al.* 1989). Thus, because sediments are the primary source of P and N to macrophytes and because they reflect both the direct effects of anthropogenic nutrient loading and the background conditions of the river, sediment P and N concentrations may be better predictors of macrophyte growth in rivers.

In this study, the relationship between sediment P and N concentrations and the growth of rooted macrophytes, in terms of both plant biomass and tissue nutrient concentrations, was examined for a Canadian prairie river. *In situ* P and N limitation and the effects on plant growth can be evaluated by quantifying the change in plant biomass (Howarth 1988) and tissue P and N concentrations (Bates 1971) to nutrient-enrichment in controlled experiments. Nutrient-enrichment studies can also provide insight into the critical P and N concentrations that result in maximum plant growth (Gerloff and Krombholz 1966). In this study, *in situ* observations were used to determine if macrophyte biomass and cover were related to distance downstream of a municipal sewage outfall and to sediment P and N concentrations. Artificial stream experiments in which sediments were enriched with a range of P and N concentrations were then conducted to determine if aquatic plants from prairie rivers are P- or N-limited and if there is a critical sediment P concentration above which aquatic plant biomass and tissue P concentrations are not further enhanced. Information on the relationship between macrophyte growth and sediment P and N concentrations in prairie rivers will allow development of environmental regulations to effectively control nuisance aquatic plant biomass.

3.1 METHODS

3.1.1 Site description

The South Saskatchewan River is a seventh order stream and a major tributary of the Saskatchewan-Nelson river system. It arises at the confluence of the Bow and Oldman Rivers in south-eastern Alberta, and flows across the semi-arid Canadian prairie ecozone to east-central Saskatchewan. In Saskatchewan, it converges with the North Saskatchewan River to form the Saskatchewan River which flows through Cedar Lake and Lake Winnipeg into the Nelson River which drains into Hudson Bay (Figure 3.1). Flows in the South Saskatchewan River are regulated by more than 20 dams in Alberta and the Gardiner Dam, located 114 km upstream of the City of Saskatoon. Mean annual flows at Saskatoon averaged 214 m^3/s from 1965 to 1986, and flows during the open-water months (April - October) averaged 183 m^3/s from 1965 to 1990 (Environment Canada 1992).

The City of Saskatoon, with a population of 186,058 (Statistics Canada 1992), is the largest municipality that discharges sewage effluent directly into the South Saskatchewan River. In 1971, Saskatoon initiated primary sewage treatment which was followed in 1985 by chlorination, to kill bacteria and thereby reduce biochemical oxygen demand. In 1990, alum precipitation was implemented with the result that total P concentrations in the effluent decreased from 6.1 ± 0.9 to 1.8 ± 0.7 mg/L (mean ± 1 SE). The sewage treatment plant was upgraded to a biological nutrient removal system in 1995 to further remove P and N.

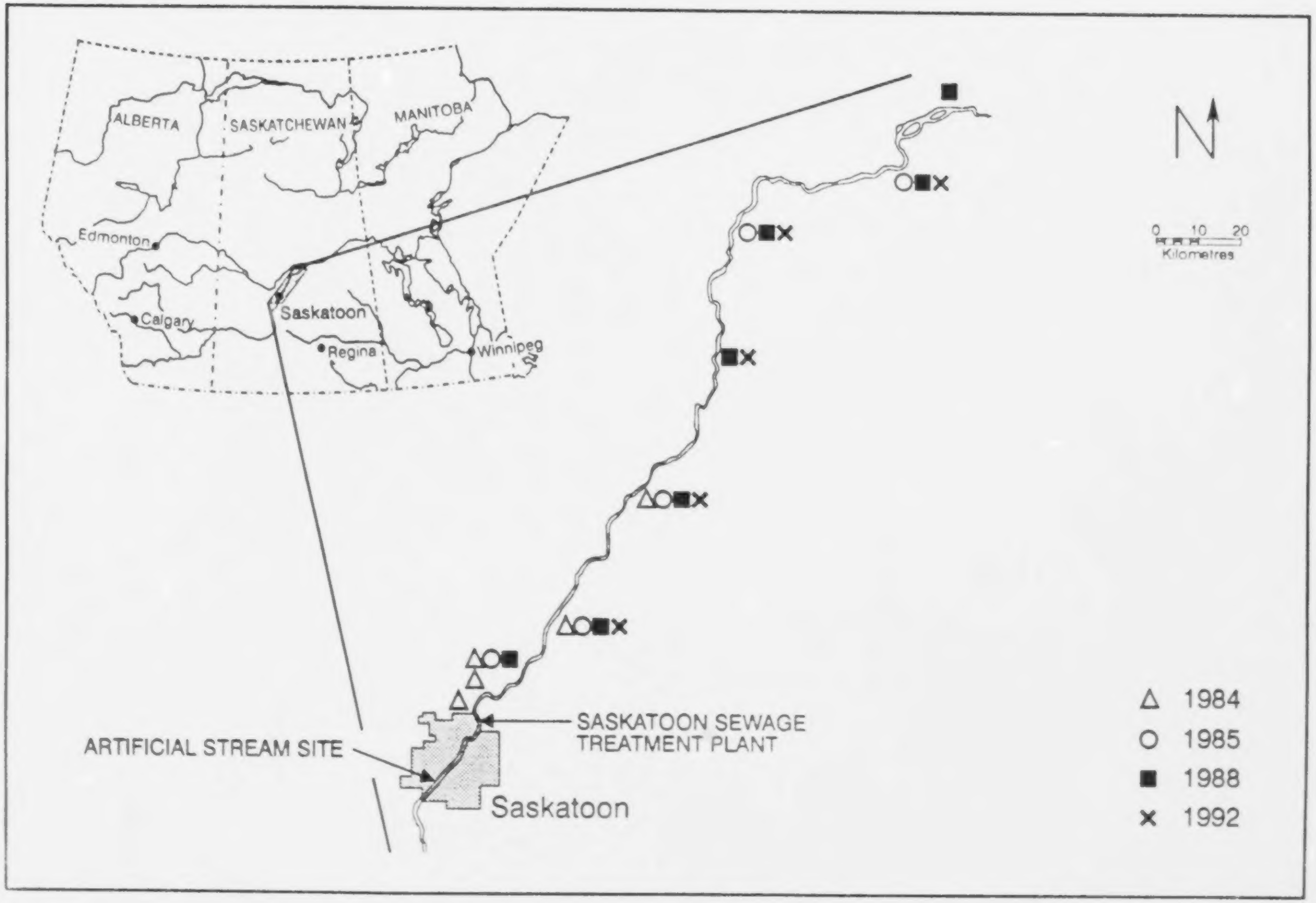

Figure 3.1: Map of the Canadian prairie provinces (inset) and the South Saskatchewan River, SK, downstream of Saskatoon. Symbols along the river indicate sites of biomass surveys in 1984, 1985, 1988, and 1992.

3.1.2 In situ Observations

Aerial surveys of the South Saskatchewan River, extending from the Saskatoon sewage treatment plant outfall to 150 km downstream, were undertaken by the City of Saskatoon in early August 1984, 1986, and 1987, to determine the percent of the river covered by submerged vegetation. Colour photographs of the river were taken from a height of approximately 300 m above the surface of the water. Macrophyte beds were identified on the photographs and selected areas were ground-truthed to ensure accurate interpretation. The extent of macrophyte cover relative to the total area of the river was determined by planimetry for 10 km river reaches. Surveys of rooted plant biomass were also undertaken in late July and early August (the period of peak biomass) 1984 and 1985 (by the City of Saskatoon; Kerc 1986), and 1988 (P.A. Chambers, unpublished data). Macrophyte biomass was evaluated at five to seven sites extending up to 150 km downstream of the Saskatoon sewage treatment plant outfall (Figure 3.1). At each site, macrophyte standing crop was harvested from either five replicate 0.165 m^2 quadrats (1984 and 1985) or ten replicate 0.1 m^2 quadrats (1988). All macrophyte samples were dried to constant mass at 80°C. In 1988, water and sediment samples were collected at each site every 7 to 14 days from June 9 to September 1. Water samples were analysed for total dissolved P and N by the Prairie and Northern Regional Water Quality Branch Laboratory, Environment Canada, Saskatoon, following procedures outlined in their manual (Environment Canada 1979). Sediment samples were analysed for exchangeable P and N by Environment Canada, at the National Hydrology Research Institute, as described in Section 3.1.4.

A detailed survey of macrophyte biomass and sediment P and N concentrations was undertaken in 1992 (P.A. Chambers, unpublished data). Ten to twenty replicates of macrophyte standing crop were harvested from 0.1 m^2 quadrats between July 28 and August 1 at five sites downstream of the Saskatoon sewage treatment plant (Figure 3.1). Samples of the upper 5 cm of sediments were collected with an Ekman dredge from within each quadrat. Plants were sorted to species, except for fine-leaved *Potamogeton* species, including *P. pectinatus*, *P. vaginatus*, *P. foliosus*, and *P. pusillus*, which were grouped. Macrophytes were dried to constant mass at 80°C and sediments were analysed for exchangeable P and N concentrations.

3.1.3 Artificial Stream Experiment

3.1.3.1 Stream design

To test the hypothesis that macrophyte biomass and tissue nutrient content are related to sediment nutrient concentrations, macrophytes were grown in two once-through aluminum artificial streams, 6 m long × 1.0 m wide × 1.0 m deep (after Gee and Bartnik 1969) in sediments enriched with either N, or P, or both. The streams were located along the South Saskatchewan River, at the City of Saskatoon Water Treatment Plant, upstream of any municipal and industrial outfalls, and oriented along a north-south axis so that shading from the sides and ends of the streams was equal across each test section over a day.

Untreated river water (except for coarse (1 cm) filtration) was pumped through a 4" polyvinyl chloride (PVC) pipe from the City of Saskatoon water treatment plant to a 1200 L head tank. The head tank dampened fluctuations in the flow of water through the streams as a result of variability in the rate of water delivery. An overflow pipe from the head tank to collecting pipes at the downstream end of the streams drained excess water. Water exited the head tank from a 6" PVC standpipe, approximately 1 m high, into a manifold that split the flow into two 4" PVC pipes that led to each stream. Water flow entering the streams was regulated with 4" gate valves. The targeted water velocity in the streams was 5 cm/s, which is consistent with velocities observed in macrophyte beds in prairie rivers (Chambers *et al.* 1991), however this was reduced when necessary to avoid damage to plant shoots caused by heavy siltation. Upon entering each stream, water passed through a collimator to reduce turbulent flow (Nowell and Jumars 1987; Vogel 1981). The collimators were constructed of plywood frames (0.2 m long × 1 m wide × 1 m deep) that encased three sheets of plastic gridding (1 cm grid diameter) spaced at equal intervals along the length of the collimators. The collimators were placed approximately 50 cm from the upstream end of each stream. Water exited the artificial streams at the downstream end of the troughs through a 60 cm high, 4" PVC standpipe, and was collected into a 6" PVC pipe that drained via a culvert to the South Saskatchewan River (Figure 3.2).

To avoid zones of turbulent flow and allow for flow deviations at the downstream end of the streams, the first 1 m and last 0.5 m were excluded from the test section of each stream. In 1995, a further 1.13 m was excluded from the upstream end of the streams due to heavy siltation and sediment deposition. To minimize boundary layer effects from the walls of the streams, 0.25 m on the sides of each stream were also excluded from the test section. To account for variation in water velocities between the upstream and downstream ends of the streams, the test sections were divided into four (three in 1995) 1.13 m long blocks. Within each test section, flows were estimated to be subcritical, with a Froude number of approximately 0.02, and turbulent, with Reynold's numbers ranging from 50,000 at the upstream end to 275,000 at the downstream end of the test sections (calculations following Craig 1993).

3.1.3.2 Experimental Design

Pilot experiments were conducted in early summer 1994 to determine the type of sediment to be used in the experiments, the most effective method for enriching the sediments, and the type and amount of N-only and P-only fertilizers required to achieve the desired range of sediment P and N concentrations. These experiments are outlined in Appendix B.

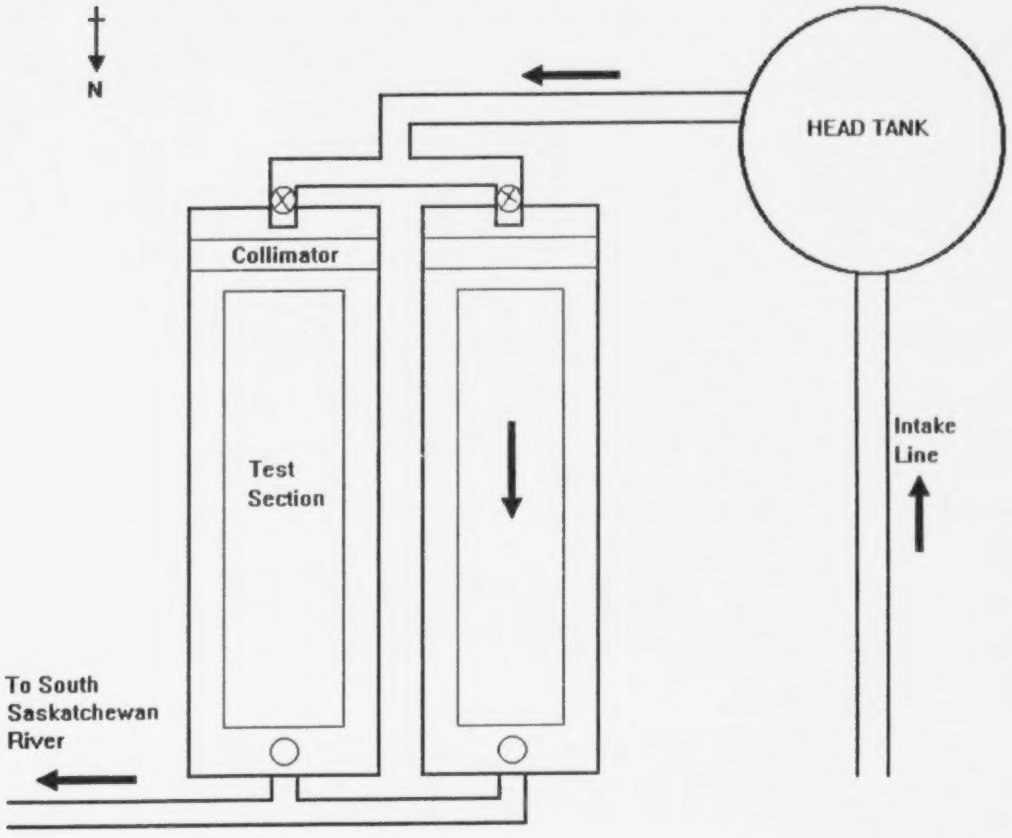

Figure 3.2: Artificial stream schematic, showing intake line, head tank, manifold and control valves, aluminum streams, collimators, and test section within each stream. Figure not drawn to scale.

To determine if macrophytes in the South Saskatchewan River are limited by the availability of either sediment P or N, *Potamogeton pectinatus*, a rooted macrophyte common in the river, was grown in the artificial streams in 1994 in one of four treatments: (1) unamended sediments, (2) P-enriched sediments, (3) N-enriched sediments, and (4) combined N + P-enriched sediments. To identify critical sediment P concentrations producing maximum macrophyte biomass, additional experiments were conducted in which *P. pectinatus* plants were grown in sediments enriched at nine P doses, ranging from approximately 40 to 1000 µg/g exchangeable P (summer 1994), or eight different P doses, ranging from approximately 60 to 300 µg/g exchangeable P (summer 1995). Trials with *Myriophyllum exalbescens* were also conducted in 1995 following the *P. pectinatus* experimental design for 1995.

For all experiments, individual plants were grown in 785 mL pots buried in a gravel bed at the bottom of the flumes. The pots were filled with sediments that were a mixture of silica sand and terrestrial soil collected near the Town of Asquith, SK, with baseline sediment P concentrations ranging from 40-60 µg/g exchangeable P and sediment N concentrations less than 1 µg/g exchangeable N (Appendix B). The sediments were enriched by mixing in known quantities of P-only fertilizer (Vigoro Super Triple Phosphate; 0-46-0), N-only fertilizer (Westco ammonium-nitrate; 34.5-0-0), or both N-only and P-only fertilizers (Appendix B). Sediments in the nutrient limitation experiment were enriched with 3.0 g of P-only fertilizer (P-enriched and N+P-enriched sediments) and 2.5 g of N-only fertilizer (N-enriched and N + P-enriched sediments). To ensure that macrophyte production was not limited by the availability of N in the critical P enrichment experiments, sediments were also enriched with N-only fertilizer to give sediment N concentrations averaging approximately 185 µg/g exchangeable N. To minimize nutrient diffusion, pots were covered with solid plastic lids except for a 2 cm^2 hole through which plant shoots could grow.

Macrophytes were collected from three sites. In 1994, *P. pectinatus* was collected from a macrophyte bed in the South Saskatchewan River, 22 km downstream of the City of Saskatoon. In 1995, growth of rooted aquatic plants in the South Saskatchewan River was inhibited due to high flows. As a result, *M. exalbescens* plants were collected from Pike Lake, SK, an oxbow lake formed from the South Saskatchewan River after the completion of the Gardiner Dam in 1965. *P. pectinatus* plants were collected in 1995 from an irrigation canal in the Eastern Irrigation District, near Brooks, AB. Water in this canal originates from the Bow River, which converges with the Oldman River to form the South Saskatchewan River. Shoot length and fresh biomass were recorded for all plants at the start of the experiments. Fresh biomass was converted to dry weight from a fresh to dry weight ratio determined for additional plants of each species from each experiment and initial plant tissue P and N concentrations were estimated from analysis of additional plants (Table 3.1). All macrophytes were transplanted into the flumes within 24 hours of collection.

Eight, ten and nine replicate pots per treatment were randomly distributed among downstream blocks in the streams for the 1994 and 1995 *P. pectinatus* and 1995 *M. exalbescens* experiments, respectively. In 1995, the two species were grown in separate streams to avoid interspecific competition.

To monitor changes in sediment chemistry over the duration of each experiment and assess if macrophytes depleted available sediment P through root-uptake, additional pots without plants were randomly placed throughout the flumes and removed at regular intervals: in 1994, three replicates of five treatments spanning the range of P additions were removed on days 1, 8, 22, and 36, and, in 1995, two replicates of three treatments were removed on days 1, 7, and 21 of the *M. exalbescens* experiment. There were no pots removed during the 1995 *P. pectinatus* experiment. Differences in sediment P concentrations between planted and unplanted pots were evaluated for all treatments at the end of each experiment.

Table 3.1: Initial characteristics of macrophytes collected for the artificial stream experiments (mean ± 1 SE). Analyses for total organic N not conducted on macrophytes from 1995 experiments.

	P. pectinatus		*M. exalbescens*
	1994	1995	1995
Biomass (g DW)	0.146 ± 0.006	0.060 ± 0.004	0.086 ± 0.003
Shoot length (cm)	16.7 ± 0.5	16.3 ± 0.5	8.7 ± 0.4
Tissue nutrients (mg/g DW)			
Total organic P	2.31 ± 0.17	1.21 ± 0.40	1.54 ± 0.23
Total organic N	28.4 ± 6.4	n/a	n/a

Current velocity in the streams was measured every 4 to 8 days throughout the experiments with a Gurly Price 1205 Mini velocity meter. Average velocity in each experimental block was calculated as the mean of three readings (measured at 60% of the total depth) across the width of the flume at the midpoint of each block. Water temperature in the head tank was monitored with a Ryan RTM2000 temperature recorder. Photosynthetically active radiation (PAR), 10 cm above the surface of the water, was recorded hourly with a LiCor Quantum sensor and datalogger throughout the 1994 experiments and from August 8 to September 22, 1995. These measurements were summed to obtain daily irradiance estimates. Water samples were collected every 4 to 8 days from the head tank and at the exit of each flume and analysed for total P (TP), total dissolved P (TDP), soluble reactive P (SRP), ammonium (NH_4), and nitrite + nitrate (NO_2 + NO_3).

The 1994 *P. pectinatus* nutrient-limitation and critical P enrichment experiments ran concurrently for 51 days from July 6 - August 22. The 1995 *M. exalbescens* experiment ran from July 6 - August 17 (43 days), while the 1995 *P. pectinatus* experiment ran for 49 days (August 5 - September 22). At the end of each experiment, macrophytes were removed from the pots, separated into above and below ground portions, and dried to constant mass at 80°C. The above-ground portion of all macrophytes was analysed for total organic P content. Sediments from all pots were collected, frozen and later analysed for exchangeable P concentrations. Due to high rates of siltation in the flumes in 1995, many plants did not survive until the end of the experiments. Macrophytes that had decomposed or lost above-ground biomass by the end of the experiments were excluded from data analysis. As a result, two treatments in the 1995 *P. pectinatus* experiment, corresponding to approximately 120 and 170 μg/g exchangeable P, were reduced to less than five replicates and these treatments were excluded from statistical analysis.

3.1.4 Analytical Methods

Water samples for TDP and SRP were filtered through pre-washed 0.45 μm membrane filters. Samples for TP and TDP were digested by Menzel and Corwin's (1965) potassium persulfate method. All P samples were analysed spectrophotometrically following the molybdenum blue colorimetric method (Murphy and Riley 1962). Samples for NH_4 in 1994 were analysed spectrophotometrically by the phenol - hypochlorite colorimetric method (Solorzano 1969). All samples for nitrite + nitrate (NO_2+NO_3) and NH_4 samples in 1995 were analysed at the University of Alberta water chemistry lab (Department of Biological Sciences) on a Technicon autoanalyser following the methods described by Stainton *et al.* (1977).

Total organic P and N in plant shoots were extracted by wet oxidation with sulphuric acid and hydrogen peroxide (Parkinson and Allen 1975) and analysed spectrophotometrically by the molybdenum blue (Stainton *et al.* 1977) and phenol-hypochlorite (Haslemore and Roughan 1976) colorimetric methods, respectively.

Exchangeable P was extracted from sediments by shaking for 16 hours with 0.1N NaOH-NaCl and measured spectrophotometrically as soluble reactive P (Stainton *et al.* 1977). Exchangeable N was extracted from sediments by shaking for 1 hour with 2M KCl (Bremner 1965) and measured spectrophotometrically as NH_4 (Haslemore and Roughan 1976).

3.1.5 Statistical analysis

Data were analysed with SPSS (1993). Regression analyses were used to determine the relationship between macrophyte biomass and sediment exchangeable P and N concentrations in the South Saskatchewan River for the 1992 survey. Biomass data in 1992 were log-transformed to stabilize variances and normalize residuals.

Differences in water chemistry, light and temperature among the three artificial stream experiments, as well as sediment chemistry over time and water velocity within each experiment, were evaluated with analysis of variance (ANOVA). *t*-tests were used to examine differences in water chemistry between the head tank and the downstream ends of the streams for each experiment and between sediment P concentrations in pots with and without plants for each treatment and experiment; a correction for unequal variances was applied when necessary (SPSS 1993). Macrophyte growth, measured as the change in plant biomass over an experiment, and tissue P concentration were evaluated in relation to sediment nutrient treatments with ANOVA. The downstream position of the plants in the streams were included as blocking factors in the ANOVA models only when significant ($P \leq 0.05$). The assumptions of normality and variance homogeneity were tested for the dependent variables with the Lilliefors and the Levene tests, respectively, and when necessary, data were analysed non-parametrically or were rank-transformed and the ranked numbers analysed parametrically (Potvin and Roff 1993). The power to detect true differences among treatment means was estimated for each analysis and when power was ≤ 0.50 (50 %) statistical tests were interpreted at $\alpha = 0.10$ to balance the probability of committing Type I and Type II errors (SPSS 1993). Reverse Helmert contrasts, where the mean of one group is compared to the mean of all preceeding groups, were used to identify differences among unamended, N-enriched, P-enriched, and N+P-enriched sediments in the nutrient limitation experiment (SPSS 1993).

While ANOVA detects differences among treatment means, it does not describe the pattern of response of a dependent variable to quantitative manipulations of an independent variable (Keppel 1991; Day and Quinn 1989). Multiple comparisons of means tests, while identifying differences among specific treatments, are inappropriate tests to use when the independent variable in the design is quantitative because they provide no information about the underlying trend in the data (Petersen 1977; Baker 1980; Dawkins 1983). Consequently, polynomial contrasts, where ANOVA treatment sums of squares are partitioned into single degree of freedom orthogonal comparisons representing linear, quadratic, cubic and higher order trends in the data were used to describe the pattern of response of aquatic plants to increasing sediment P treatments (Day and Quinn 1989; Sokal and Rohlf 1981; Keppel 1991). The significance of each contrast was tested against the residual mean square error with the F - distribution (SPSS 1993). A significant linear trend in the data implies that there are no inflections in the pattern of response, while a quadratic trend indicates the presence of one inflection in the response-curve (taking the shape of a parabola) (Keppel 1991). While the only limitation in the number of trends that can be detected is the number of treatment groups, there is little biological theory to guide the interpretation of higher-order trends and consequently interpretation of the contrasts was not taken beyond the quadratic component (Keppel 1991). When trend components were significant, a regression curve that related macrophyte biomass or tissue P concentrations to sediment P enrichment was constructed. The points on the curve were calculated such that the predicted mean for each treatment equalled the grand mean of the dependent variable plus the product of the calculated slope of the line and the trend coefficient generated for each treatment and contrast (linear or quadratic) (Table 3.2) (Keppel 1991). Linear and quadratic regressions were combined when both were significant. The polynomial coefficients were constructed to include unequal spacing of the treatments and unequal replication (Table 3.2) (Robson 1958; Cohen 1980; SPSS 1993).

3.2 RESULTS

3.2.1 In situ Observations

Macrophyte cover in the South Saskatchewan River was negligible upstream of the Saskatoon sewage treatment plant, increased for a distance up to 60 km downstream of the plant and thereafter declined (Figure 3.3). Cover was low in 1986, however discharge in the South Saskatchewan River at Saskatoon was high during the open-water months of this year relative to the other years surveyed (Table 3.3). While the distance at which

Table 3.2: Linear (C_L) and quadratic (C_Q) coefficients used to construct polynomial contrasts for all experiments. Treatment names refer to quantity (in grams) of P-only fertilizer added to sediments. Coefficients are orthogonal and have been constructed to include unequal treatment spacing.

	P. pectinatus 1994		*P. pectinatus* 1995		*M. exalbescens* 1995	
Treatment	C_L	C_Q	C_L	C_Q	C_L	C_Q
0P	-0.467	0.514	-0.463	0.517	-0.460	0.521
0.1P	-	-	-0.352	0.096	-0.351	0.176
0.2P	-	-	-0.241	-0.232	-0.243	-0.091
0.3P	-	-	-	-	-0.135	-0.282
0.4P	-	-	-0.019	-0.610	-0.027	-0.396
0.5P	-0.359	0.198	-	-	-	-
0.6P	-	-	-	-	0.186	-0.391
0.8P	-	-	0.426	-0.253	0.406	-0.079
1.0P	-0.252	-0.047	0.649	0.483	0.622	0.542
1.5P	-0.144	-0.221	-	-	-	-
2.0P	-0.036	-0.323	-	-	-	-
2.5P	0.072	-0.354	-	-	-	-
3.0P	0.180	-0.313	-	-	-	-
4.0P	0.395	-0.017	-	-	-	-
5.0P	0.611	0.564	-	-	-	-

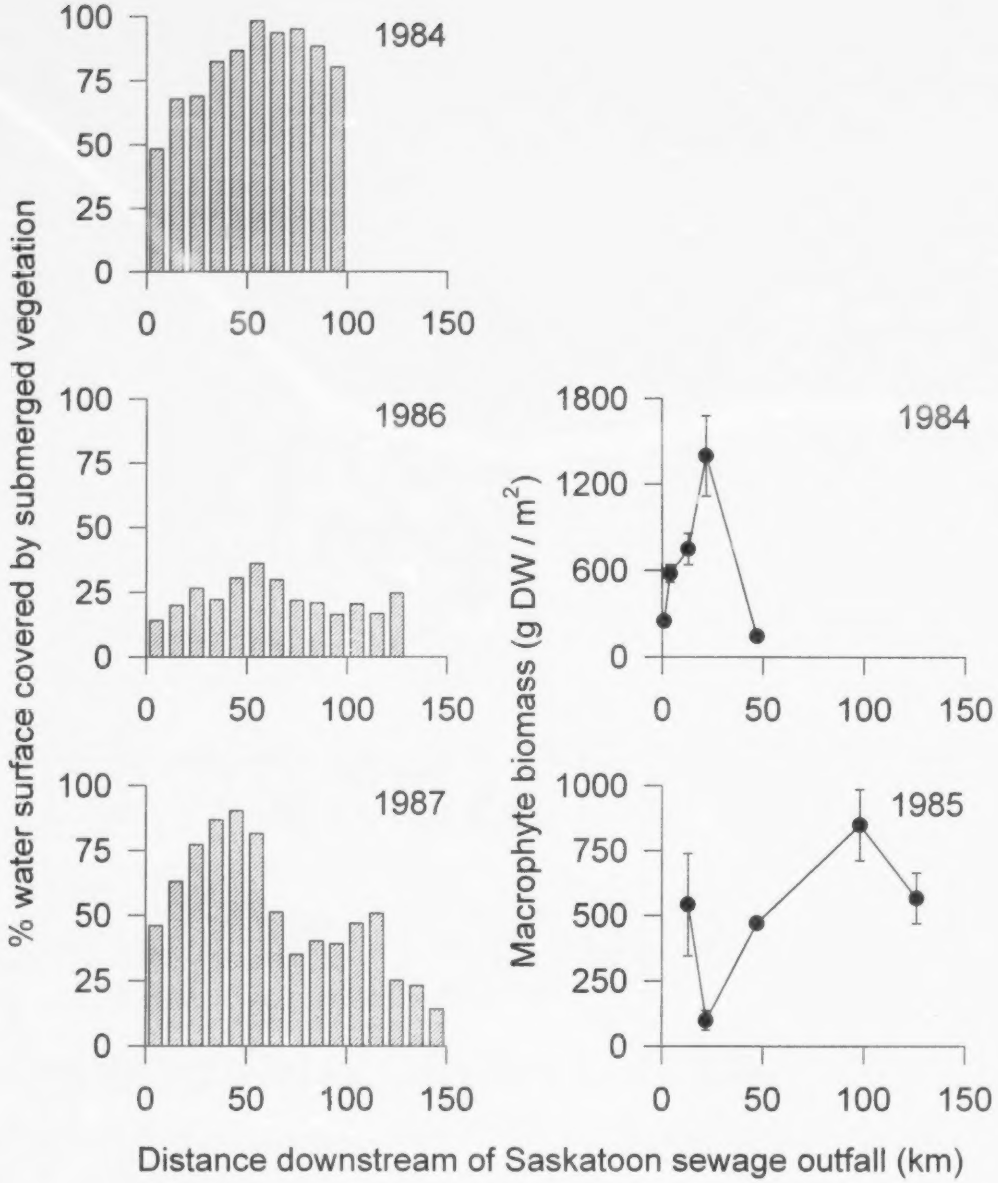

Figure 3.3: Percent macrophyte cover (left column) and macrophyte biomass (right column) in the South Saskatchewan River, downstream of the Saskatoon sewage treatment plant from 1984 to 1987. Biomass data presented as mean ± 1 SE.

Table 3.3: Discharge in the South Saskatchewan River at Saskatoon averaged for the open-water months (April - October) and annually. Mean (± 1 SE) discharges in the river since the completion of the Gardiner Dam upstream of Saskatoon are also presented (1965-1986) (Environment Canada 1992). "n/a" means not available due to missing winter data.

Year	April - October discharge (m^3/s)	Annual discharge (m^3/s)
1984	56	85
1985	66	92
1986	170	202
1987	97	n/a
1988	51	n/a
1965-1986	183 ± 23	214 ± 15

maximum biomass was observed varied among years (from 25 to 100 km downstream), the pattern in the data was similar to the cover data with cover and biomass increasing from zero upstream of the Saskatoon sewage treatment plant to a maximum downstream of the city and declining further downstream (Figure 3.3). In 1988, biomass reached a maximum approximately 75 km downstream of the sewage treatment plant while open-water and sediment exchangeable P and N concentrations peaked 25 km downstream of the outfall and declined further downstream (Figure 3.4).

Macrophyte biomass in 1992 ranged from 4 to 577 g/m^2 and was correlated with sediment P concentrations ($F_{2,95} = 19.87$, $P < 0.0001$). This relationship was best described by a quadratic fit through the data, explaining 28% of the variability in biomass (Figure 3.5). Biomass was not related to sediment N concentrations ($P \geq 0.06$ tor linear and quadratic regressions) (Figure 3.5).

3.2.2 Artificial Stream Experiments

3.2.2.1 Background conditions

Water temperature in the head tank differed among all experiments, and was highest in the 1994 *P. pectinatus* experiment ($F_{2,13796} = 5428$, $P < 0.0001$) (Table 3.4). Daily PAR in 1994 averaged 41.1 E/m^2 and was greater than during both the 1995 experiments ($F_{2,103} = 13.35$, $P < 0.0001$). Irradiance did not differ among the two 1995 experiments ($P > 0.05$, LSD). Open-water concentrations of phosphorus (TP, TDP, and SRP) and nitrogen (NH_4 and NO_2+NO_3) did not differ between the head tank and the downstream ends of the artificial streams for all experiments ($P > 0.12$). TP and SRP concentrations did not differ among experiments ($P > 0.10$), while TDP concentrations in the 1994 *P. pectinatus* experiment were higher than in both 1995 experiments ($F_{2,61} = 12.65$, $P < 0.0001$). NH_4 and NO_2+NO_3 concentrations varied among experiments ($F_{2,61} = 7.93$, $P = 0.0009$ and $F_{2,59} = 21.17$, $P < 0.0001$), and were lowest in the 1995 and 1994 *P. pectinatus*

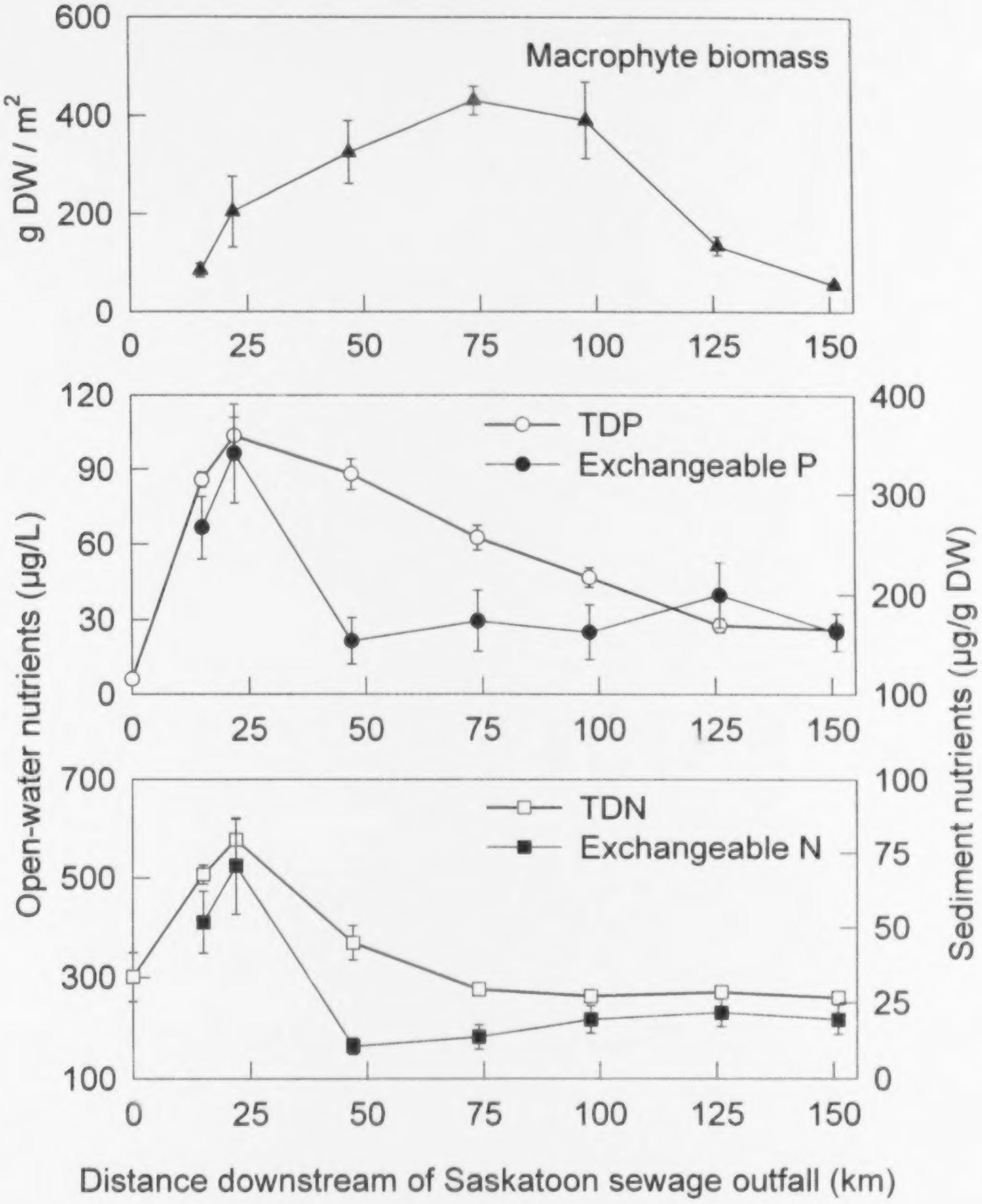

Figure 3.4: Macrophyte biomass (top panel) in early August, and mean seasonal P (middle panel) and N (bottom panel) concentrations in the South Saskatchewan River, downstream of the Saskatoon treatment plant in 1988. Open-water (open symbols) and sediment (solid symbols) nutrients are presented. All data are mean ± 1 SE.

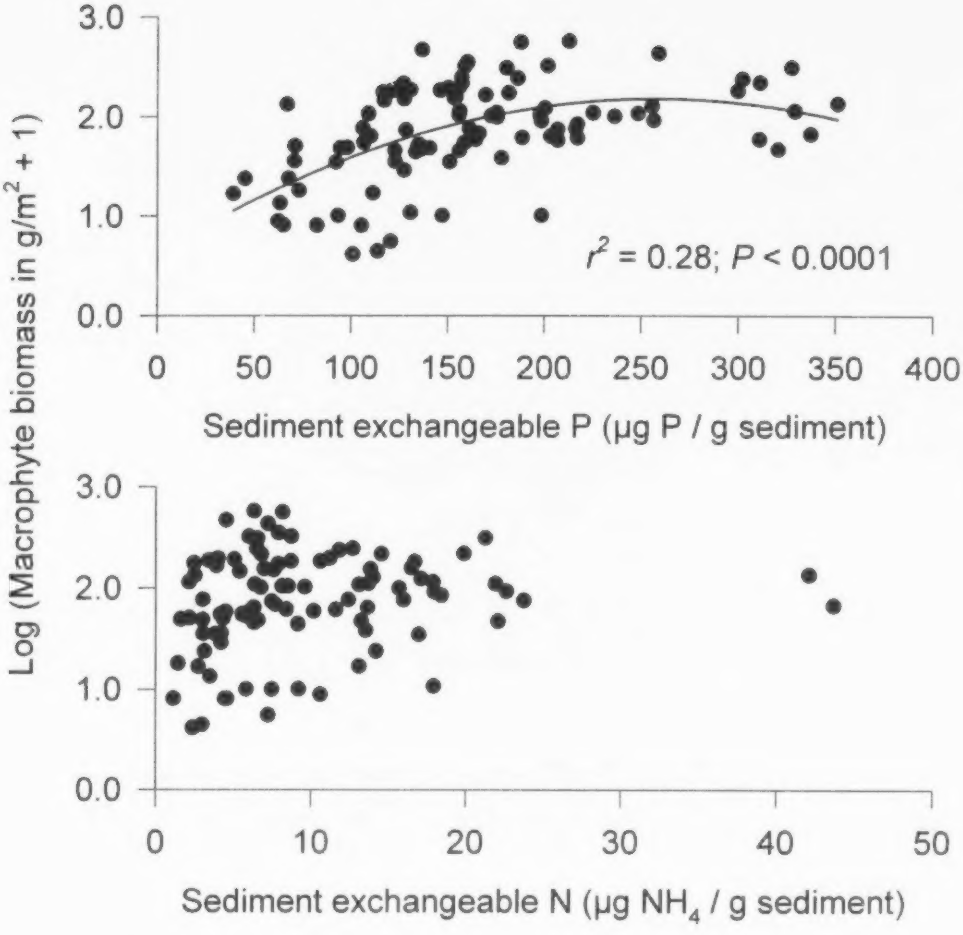

Figure 3.5: Macrophyte biomass (log-transformed) plotted against sediment P (top) and N (bottom) concentrations. Samples collected in 1992 in the South Saskatchewan River, downstream of the Saskatoon sewage treatment plant.

Table 3.4: Background conditions of artificial stream experiments. Data presented as mean ± 1 SE.

	P. pectinatus		*M. exalbescens*
Parameter	1994	1995	1995
Water temperature (°C)	21.24 ± 0.03	16.36 ± 0.04	17.28 ± 0.03
Daily PAR (E/m^2)	41.1 ± 1.6	31.6 ± 1.6*	24.9 ± 4.7*
Stream water chemistry			
TP	31 ± 4	20 ± 1	26 ± 2
TDP	13 ± 2	4.7 ± 0.2	4.7 ± 0.5
SRP	2.3 ± 0.2	2.6 ± 0.3	2.6 ± 0.6
NH_4	14 ± 2	5.1 ± 1.6	14 ± 3
NO_2+NO_3	102 ± 10	186 ± 10	135 ± 14
Discharge (m^3/day·flume)	1800 ± 140	≤ 270	1300 ± 420
Stream velocity (m/s)	0.034 ± 0.001	≤ 0.012	0.043 ± 0.005

*PAR in 1995 averaged from Aug. 8 - 17 for *M. exalbescens* experiment and from Aug. 8 - Sept. 22 for *P. pectinatus* experiment.

experiments, respectively. Water velocity in the streams was higher in the upstream than the downstream blocks for all experiments, and discharges were highest in the 1994 *P. pectinatus* experiment. To minimize damage to plant shoots caused by heavy siltation, velocity and discharge were maintained low (below detection limits) for the 1995 *P. pectinatus* experiment (Table 3.4).

Sediment exchangeable P concentrations in pots with plants were linearly related to the quantity of P-only fertilizer added for all experiments (Figure 3.6). Sediment P concentrations in pots without plants did not vary over the duration of the 1994 *P. pectinatus* experiment or the 1995 *M. exalbescens* experiment ($P > 0.05$; non-parametric ANOVA). Moreover, at the end of the experiments, sediment P concentrations did not differ ($P > 0.05$; *t*-test) between pots with and without plants except for the lowest P-enrichment treatment (corresponding to ≈ 45 μg/ g exchangeable P) in the 1994 *P. pectinatus* experiment and the 0.8P treatment (corresponding to ≈ 210 μg/g exchangeable P) in the 1995 *P. pectinatus* experiment which were less in pots with plants than without plants ($P \leq 0.019$; *t*-test).

3.2.2.2 Sediment nutrient limitation

P. pectinatus growth, expressed as the change in biomass of the 1994 experiment, differed among unamended, N-enriched, P-enriched, and N+P-enriched sediments ($F_{3,35}$ = 3.54, $P = 0.024$; ANOVA on rank-transformed data) (Table 3.5). Biomass was greatest on the N+P-enriched sediments, lowest on unamended and N-enriched sediments, and intermediate on the P-enriched sediments (Figure 3.7). There was no difference in biomass between the unamended and N-enriched sediments ($P = 0.721$; Reverse Helmert contrast). Biomass on the P-enriched sediments was greater than the combined biomass on N-enriched and unamended sediments ($P = 0.097$; Reverse Helmert contrast interpreted at $\alpha = 0.10$ because of low power), and biomass on the N+P-enriched

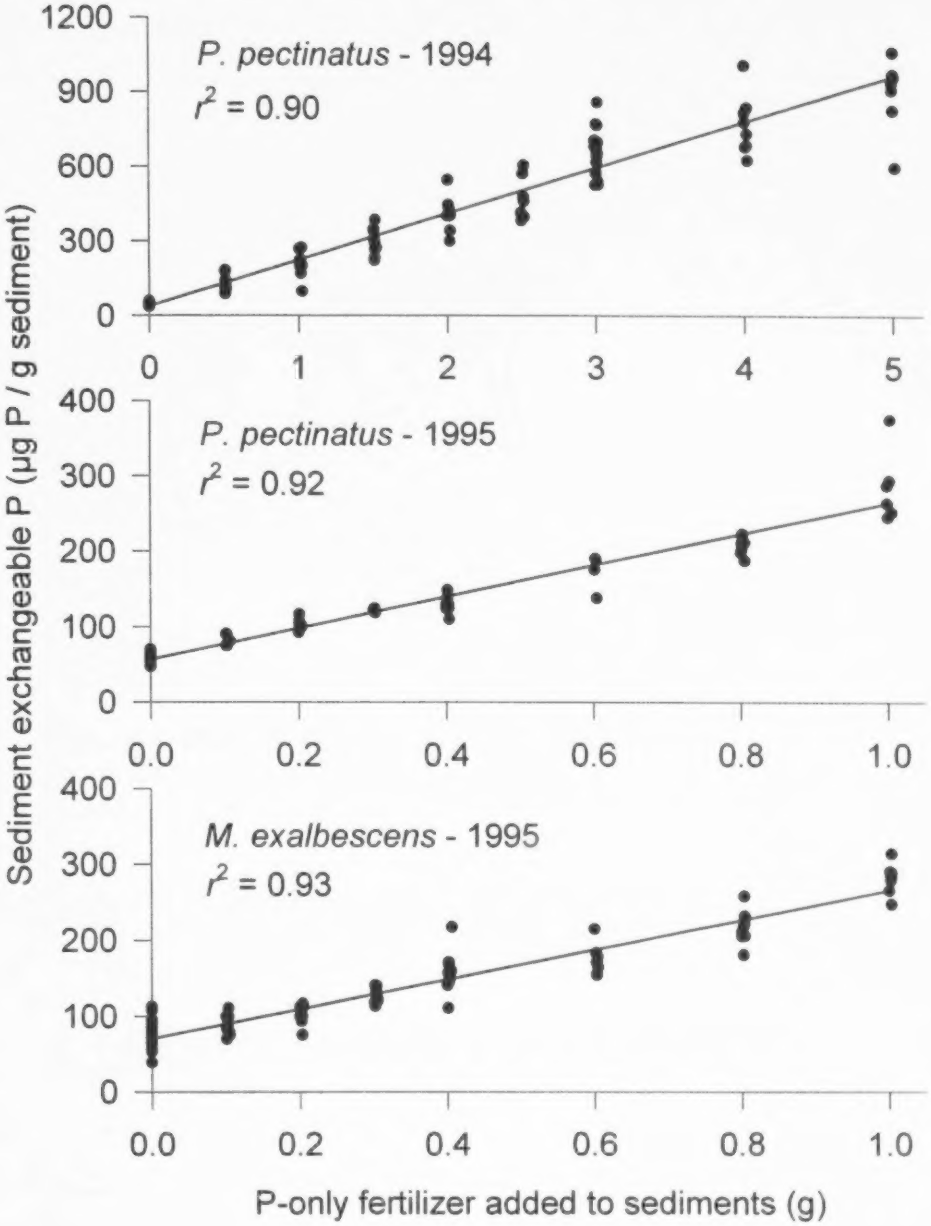

Figure 3.6: Relationship between quantity of P-only fertilizer added to sediments and exchangeable P concentrations in pots with plants for all artificial stream experiments. All regressions significant at $P \leq 0.0001$.

Table 3.5: Analysis of variance table for change in biomass in relation to sediment type (unamended, N-enriched, P-enriched, N+P-enriched) in the nutrient limitation experiment, with Reverse Helmert contrasts.

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	1149	3	383	3.54	0.024
N vs unamended	14	1	14	0.13	0.721
P vs N & unamended	315	1	315	2.91	0.097
N+P vs P, N, & unamended	820	1	820	7.57	0.009
Residual Error	3791	35	108		
Total	4940	38			

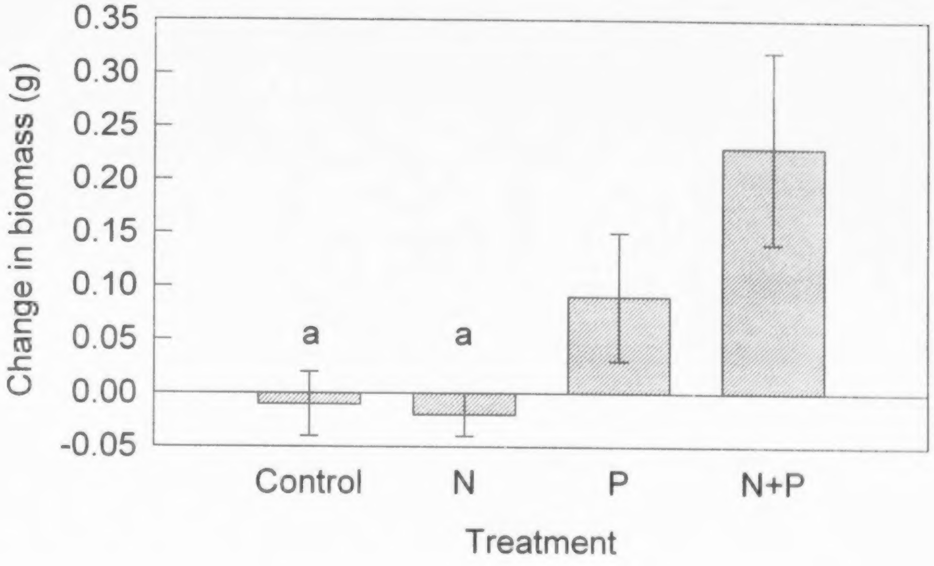

Figure 3.7: Change in biomass for unamended (Control), N-enriched (N), P-enriched (P), and N+P-enriched (N+P) sediments. Bars sharing the same letter are not different ($P > 0.05$; paired contrast). Data presented as mean ± 1 SE.

sediments was greater than biomass on unamended, N-enriched, and P-enriched sediments ($P = 0.009$; Reverse Helmert contrast) (Table 3.5, Figure 3.7).

3.2.2.3 Critical sediment P concentrations resulting in maximum growth

Growth of *P. pectinatus* in the 1994 experiment increased with increasing concentrations of sediment P (Figure 3.8). While there was no overall difference in the change in plant biomass among treatments ($P = 0.165$; ANOVA), a linear trend in the data was evident ($P = 0.003$) with biomass increasing with sediment P concentrations (Table 3.6). Over a narrower range in sediment P (the 1995 *P. pectinatus* experiment), there were no differences in biomass among treatments ($P > 0.05$; ANOVA) and no trend component to the data when interpreted at $\alpha = 0.05$ (Table 3.6, Figure 3.8). The power to detect true differences in biomass among treatments for the 1995 experiment was, however, very low (22%), and a linear trend was evident when interpreted at $\alpha = 0.10$ (Table 3.6). Growth of *M. exalbescens* differed among the P-amended sediments ($P = 0.025$; ANOVA) and increased linearly with sediment P concentrations (Table 3.6, Figure 3.8).

While the overall biomass response of *P. pectinatus* to sediment P enrichment was not different among treatments (Table 3.6), tissue P concentrations differed ($P \leq 0.023$; ANOVA) among the sediment P groups for both the 1994 and 1995 experiments (Table 3.7). Over a 900 μg/g span in sediment exchangeable P concentrations (the 1994 experiment), linear and quadratic trends with increasing sediment P concentrations were observed in plant tissue P concentrations (Table 3.7, Figure 3.9), while over a finer scale (60-300 μg/g exchangeable P; the 1995 experiment) linear and quadratic trends were evident in tissue P concentrations when interpreted at $\alpha = 0.10$ (because of low power) (Table 3.7, Figure 3.9). Tissue P concentrations of *M. exalbescens* also differed with sediment P enrichment ($P < 0.001$; ANOVA; Table 3.7) and linear and quadratic components ($P \leq 0.002$) in the pattern of increase were evident (Table 3.7, Figure 3.9).

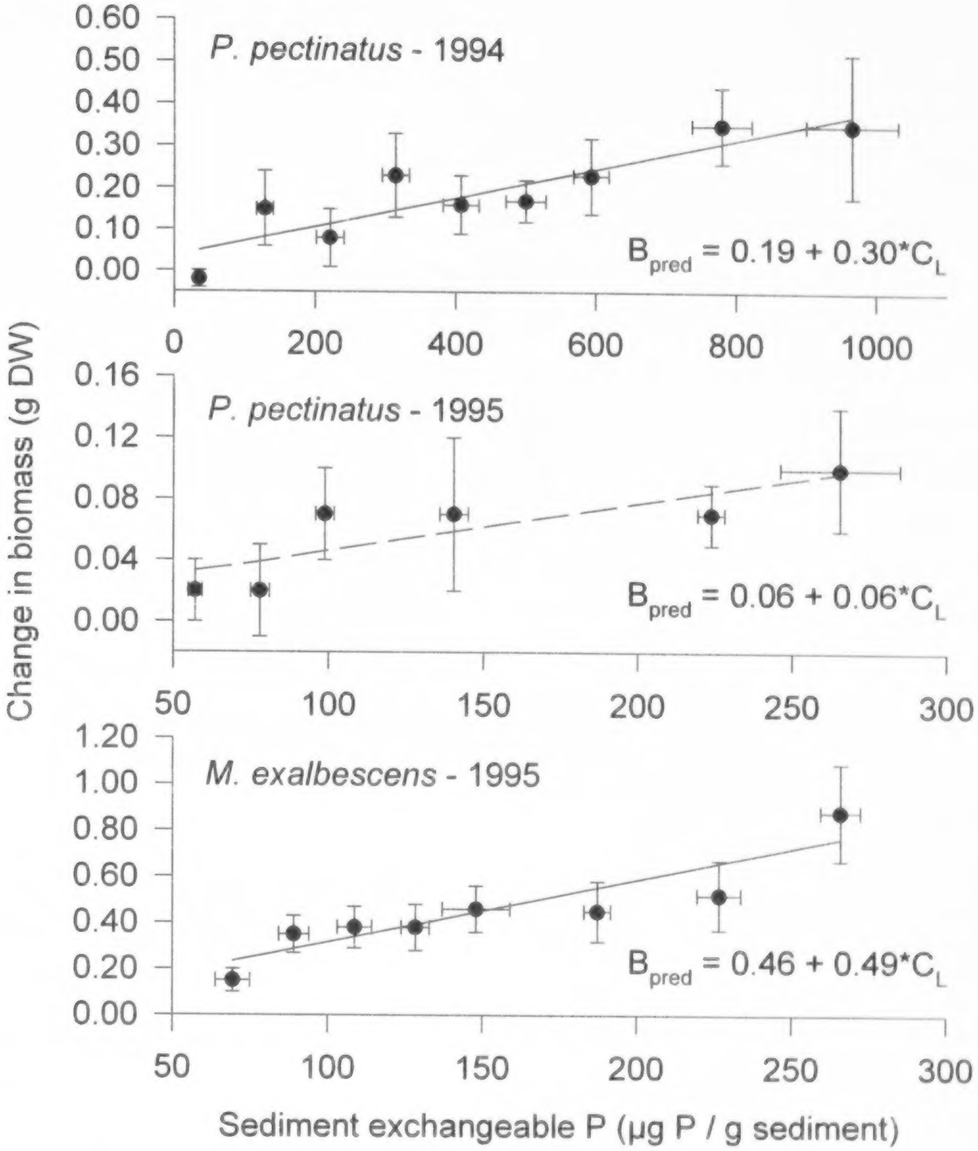

Figure 3.8: Change in biomass (mean ± 1 SE) versus sediment exchangeable P for all artificial stream experiments. Lines represent predicted biomass (B_{pred}) and are based on results of polynomial contrasts and linear contrast coefficients (C_L) from Table 3.2. Dashed lines interpreted at $\alpha = 0.10$ due to low statistical power.

Table 3.6: Analysis of variance tables for change in biomass in relation to P addition, with polynomial contrasts.

a) *P. pectinatus* 1994

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	0.92	8	0.11	1.52	0.165
Linear	0.74	1	0.74	7.76	0.003
Quadratic	0.01	1	0.01	0.11	0.747
Residual Error	5.28	70	0.08		
Total	6.20	78			

b) *P. pectinatus* 1995

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	0.03	5	0.01	0.87	0.512
Linear	0.02	1	0.02	2.97	0.094
Quadratic	< 0.01	1	< 0.01	0.14	0.711
Residual Error	0.24	33	0.01		
Total	0.27	38			

c) *M. exalbescens* 1995

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	2.25	7	0.32	2.57	0.025
Linear	1.79	1	1.79	14.32	< 0.001
Quadratic	0.03	1	0.03	0.28	0.601
Residual Error	5.62	45	0.12		
Total	7.88	52			

Table 3.7: Analysis of variance table for tissue P concentrations in relation to P additions, with polynomial contrasts.

a) *P. pectinatus* 1994

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	79.54	8	9.94	4.11	0.001
Linear	49.12	1	49.19	20.29	< 0.001
Quadratic	18.84	1	18.84	7.78	0.007
Residual Error	135.56	56	18.84		
Total	215.10	64			

b) *P. pectinatus* 1995

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	23.42	5	4.68	3.06	0.023
Linear	14.55	1	14.55	9.56	0.004
Quadratic	5.90	1	5.90	3.85	0.058
Residual Error	49.00	32	1.53		
Total	72.42	37			

c) *M. exalbescens* 1995

Source of Variation	*SS*	*df*	*MS*	*F*	*P*
Treatment	92.83	7	13.26	25.30	< 0.001
Linear	82.15	1	82.15	156.7	< 0.001
Quadratic	5.79	1	5.79	11.04	0.002
Residual Error	23.59	45	0.52		
Total	116.4	52			

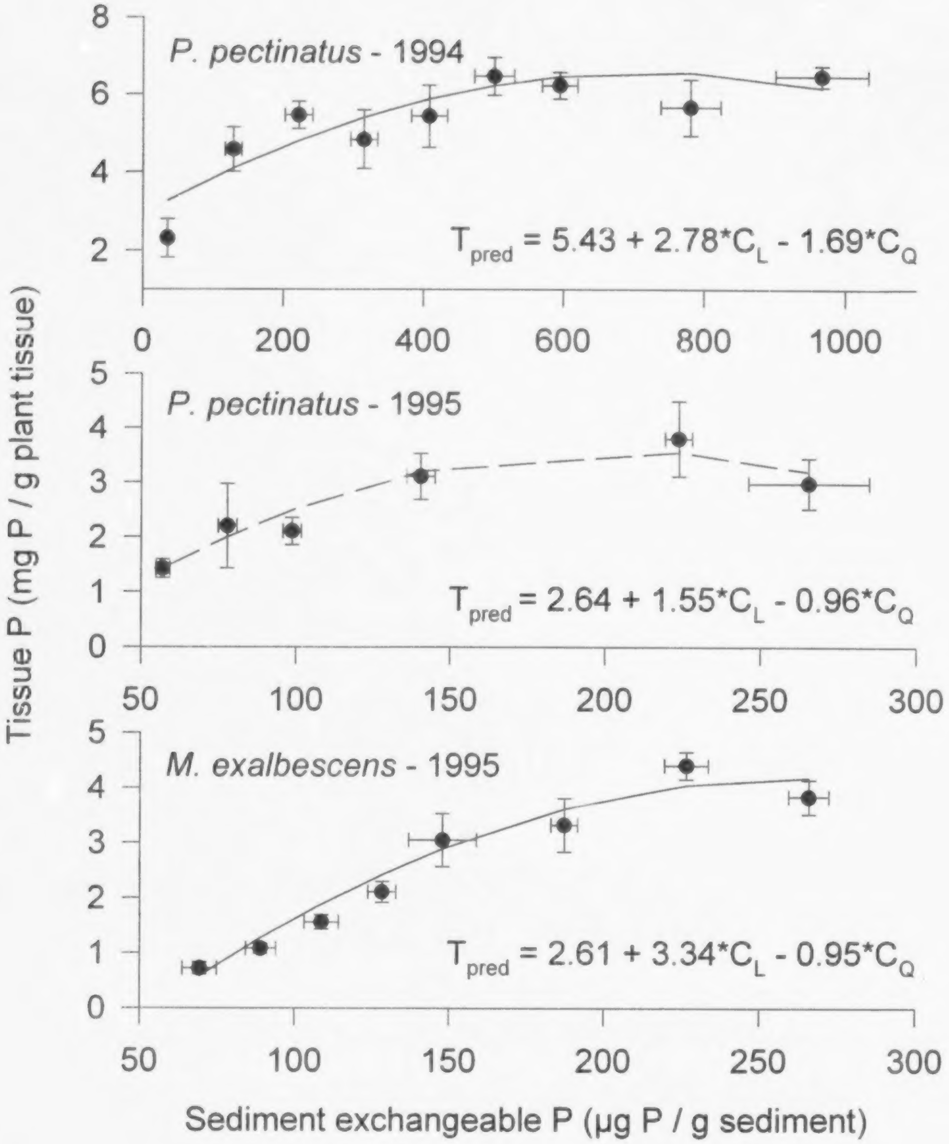

Figure 3.9: Tissue P (mean ± 1 SE) versus sediment exchangeable P concentrations for all artificial stream experiments. Lines represent predicted tissue P (T_{pred}) and are generated from polynomial contrasts and linear (C_L) and quadratic (C_Q) contrast coefficients from Table 3.2. Dashed lines interpreted at $\alpha = 0.10$ due to low statistical power.

3.3 DISCUSSION

Field observations of macrophyte biomass and cover in the South Saskatchewan River conducted from 1984 to 1988 demonstrated that plant growth increased downstream of the City of Saskatoon sewage treatment plant and lend support to the belief that anthropogenic nutrient loading to aquatic systems increases plant production (Wong *et al.* 1979; Werner and Weise 1982). Macrophyte cover was, in general, negligible upstream of the Saskatoon sewage outfall, peaked at approximately 60 km downstream and declined with distance further downstream (Figure 3.3). Low cover in 1986 can be attributed to high discharges in the river relative to the other years surveyed (Table 3.3). A similar pattern to the cover data was observed in macrophyte biomass, albeit with greater interannual variability, with increasing biomass up to 100 km downstream of the sewage treatment plant, followed by a decline in biomass further downstream (Figure 3.3). Comparison of biomass and nutrient concentrations in 1988 revealed that biomass reflected the patterns in open-water and sediment P and N concentrations, with peak biomass occurring 50 km further downstream than the site of peak nutrient concentrations (Figure 3.4). More detailed survey data from 1992 revealed that sediment exchangeable P concentrations explained 28% of the variability in macrophyte biomass in the South Saskatchewan River (Figure 3.5).

The observation of increased submerged vegetation downstream of the Saskatoon sewage outfall is consistent with reports of effluent-enhanced submerged vegetation in the Tees River, England (Butcher 1933), the Great Stour River, England (Fox *et al.* 1989), and the Bow River, Alberta (Chambers *et al.* 1991). However, macrophyte growth was not related to nutrient-enrichment in the Crnojevića River, Yugoslavia (Smith *et al.* 1978), the River Ivel, England (Owens and Edwards 1961), the Holston River, Tennessee (Peltier and Welch 1989) or Badfish Creek, Wisconsin (Madsen and Adams 1988), suggesting that macrophyte-nutrient relationships are confounded by other factors that have been demonstrated to influence submerged plant growth (Madsen and Adams 1988;

Owens and Edwards 1961). Thus, the low explanatory power of the 1992 biomass-sediment nutrient relationship (Figure 3.5) may be due to site-specific differences among factors such as sediment type, texture and organic matter content (Barko *et al.* 1986), herbivory (Sheldon 1987; Lodge and Lorman 1987), current velocity within macrophyte beds (Chambers *et al.* 1991), or light availability (Peltier and Welch 1969; Canfield and Hoyer 1988).

Artificial streams were employed to isolate the effects of sediment P and N on aquatic macrophytes from other potentially confounding factors. Historically, artificial streams have been used to determine the relationship between algal production and nutrients in lotic systems (Bothwell 1993), and the benefits offered by an artificial stream approach, such as increased environmental control and increased treatment diversity and replication, can also be applied to macrophyte studies (see Lamberti and Steinman 1993 for review). In my experimental stream design, compromises were necessary to accommodate the depth of water needed to grow rooted macrophytes and simulate velocities typical of macrophyte beds in the South Saskatchewan River. Thus, the streams used in this study were narrower than the width to depth ratio of five recommended to avoid irregular flows caused by boundary layers along the walls of the streams (Nowell and Jumars 1987), and water velocities were generally slower than the targeted 5 cm/s due to limitations in the rate of water delivery and high rates of siltation in 1995 (Table 3.4). These compromises were offset, however, by the benefits gained by locating the streams adjacent to the South Saskatchewan River, upstream of any municipal and industrial sewage outfalls, and by supplying natural river water to the system under conditions of ambient light and temperature.

Results from the artificial stream experiments revealed that biomass of *P. pectinatus* plants was enhanced with the addition of P-only fertilizer, and further enhanced with the addition of P-only and N-only fertilizers in combination, suggesting that plant growth in the South Saskatchewan River is primarily limited by the availability of P and, when P is in excess, secondarily limited by N availability (Figure 3.7). These results are consistent with observations made *in situ* in 1992, namely that macrophyte biomass was related to sediment P but not N concentrations (Figure 3.5). Moreover, the artificial stream P-enrichment experiments demonstrated that over a broad range of sediment P concentrations, biomass of *P. pectinatus* and *M. exalbescens* increased linearly with sediment P and a saturation point was not reached (Figure 3.8). However, tissue P concentrations for all experiments increased linearly up to a critical sediment P range of 200-450 µg/g exchangeable P, beyond which tissue P was not enhanced (Figure 3.9). These critical P concentrations represent the plants' physiological optima with respect to sediment P (Ernst 1978), and maximum macrophyte biomass in the South Saskatchewan River in 1992 was reached near the physiologically optimal concentration of approximately 200 µg/g exchangeable P (Figure 3.5). However, the 1988 biomass survey revealed that macrophyte biomass was not maximal throughout the portion of the South Saskatchewan River where sediment P concentrations were above 200 µg/g exchangeable P (approximately 15 to 100 km downstream of the sewage treatment plant), indicating that macrophytes in the South Saskatchewan River are constrained by additional factors and do not achieve maximum biomass over the entire geographic range where sediment P conditions are optimal (Figure 3.4). It is possible that macrophytes growing closest to the Saskatoon sewage treatment plant are constrained by high dissolved N concentrations in the open-water. It has been demonstrated that open-water N concentrations influence macrophyte community assemblages in streams of the Upper Rhine plain, Alsace (Carbiener *et al.* 1990) and they are negatively correlated with macrophyte biomass in lakes and rivers worldwide (Chapter 2). Furthermore, invertebrate abundance may be higher closer to the sewage treatment plant, thereby increasing grazing pressure on aquatic plants and maintaining biomass low despite optimal sediment P concentrations.

Studies such as this one that have attempted to relate estimates of macrophyte growth in rivers to P and N concentrations in the surrounding environment (water or sediments) have yielded contradictory results probably because of the interactive effects of physical (light availability, temperature, flow), chemical (pH, micro-nutrients, dissolved oxygen), and biological (tissue decay, competition, herbivory) factors (Wong and Clark 1976). For example, macrophyte growth was P-limited in rivers of Southern Ontario (Wong and Clark 1976), the Grand River, Ontario (Walker *et al.* 1979), Spring Creek, Pennsylvania (Wright and McDonnell 1986*a*) and the River Hull, England (Carr and Goulder 1990). In contrast, the growth of macrophytes in 19 streams in Denmark was limited primarily by factors other than nutrient availability such as variable discharge rates and variations in sediment texture (Kern-Hanson and Dawson 1978). The macrophyte *Myriophyllum aquaticum* in drainage canals and lakes of northern California was limited by the availability of N, P, or neither nutrient depending on location (Sytsma and Anderson 1993), while studies of macrophyte growth in eutrophic streams (i.e. where P and N are present in excess) have generally found that light availability and water temperature are the primary determinants of growth (Peltier and Welch 1969). For example, macrophyte growth is not limited by nutrient availability in eutrophic streams in Florida (Canfield and Hoyer 1988), Little Conesus Creek, New York (Peverly 1979), Badfish Creek, Wisconsin (Madsen and Adams 1989), and the Crnojevića River, Yugoslavia (Smith *et al.* 1978). Thus, while macrophytes in some rivers are limited by P and N availability, the general picture of the macrophyte-nutrient relationship is one of poor predictability both within specific rivers (this study) and among many rivers spanning a broad geographic range (Chapter 2). This poor predictability of biomass based on P and N concentrations indicates that macrophyte growth is constrained by many contrasting factors that are not easily quantified.

The variability in macrophyte response to nutrient addition makes it difficult to set environmental guidelines for nutrient release to control submerged plant biomass. *In situ* investigations and controlled experiments demonstrated that macrophyte growth in the South Saskatchewan River is enhanced downstream of the City of Saskatoon's sewage treatment plant, primarily due to increased sediment P availability. Thus, nutrient control will result in reduced macrophyte biomass in the river, but the extent of the reduction is difficult to quantify primarily because of the low predictive power of the *in situ* sediment exchangeable P and biomass relationship (Figure 3.5). Other studies have likewise demonstrated that open-water concentrations of P and N are poor predictors of periphyton, epiphyton, and macrophyte biomass in rivers (Chapter 2; Jones *et al.* 1984; Kern-Hanson and Dawson 1978; Canfield and Hoyer 1988; Peltier and Welch 1969). Thus, while management strategies aimed at controlling phytoplankton production in lakes have been successful by focusing on open-water P and N concentrations, this approach may work in some specific situations but won't necessarily apply to all rivers. The current approach being adopted or reviewed by agencies from across North America is to regulate primary production in terms of the plants themselves and not P and N concentrations (Nordin 1985; Health and Welfare Canada 1992; Saskatchewan Environment 1988; Ministère de l'Environnement du Québec 1992; U.S.EPA 1988*a* and 1988*b*). Thus, while P and N reductions in Saskatoon's sewage effluent will lower macrophyte biomass downstream of the city, the magnitude of the decrease cannot be well-predicted because of the interactive effects of factors other than sediment P, such as invertebrate grazing, flow differences, and interannual variability, on macrophyte growth. Furthermore, there is only limited information on the relationship between open-water and sediment P and N loads and on the lag time between nutrient reductions in the open-water and lowered sediment nutrient concentrations. Therefore, the management of rooted macrophytes in prairie rivers should integrate long-term reductions in municipal nutrient loading and short-term control of undesirable biomass through manual harvesting techniques.

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Chapter 4: Synthesis

4.0 SYNTHESIS

The aim of this research was to quantify the relationship between phosphorus (P) and nitrogen (N) in freshwater systems and the abundance of rooted aquatic plants. The role of these nutrients in regulating macrophyte abundance, particularly in lotic environments, is poorly understood. Some studies have found that macrophytes are either P or N-limited and that abundance increases in response to nutrient enrichment (*e.g.* Carr and Goulder 1990; Anderson and Kalff 1986), whereas other studies have demonstrated that macrophyte abundance is not related to P and N concentrations in either the open-water or sediments (Canfield and Hoyer 1988; Kern-Hansen and Dawson 1978). To address my objective and to clarify the conflicting reports in the literature, two main projects were undertaken. The first project examined the relationship between macrophyte biomass and open-water concentrations of P and N in lakes and rivers worldwide with data published in the literature (Chapter 2). The second project integrated *in situ* observations and artificial stream experiments to determine how sediment P and N concentrations regulate growth of submerged aquatic plants in the South Saskatchewan River, Saskatchewan and to make recommendations regarding the management of rooted macrophytes in prairie rivers (Chapter 3).

On a global scale, approximately 30% of the variability in macrophyte biomass was explained by some form of both P and N and the type of waterbody (lake or river). Macrophyte biomass was positively correlated to concentrations of P and negatively correlated to concentrations of N in the open water, suggesting that there is an optimal combination of these nutrients that results in maximum biomass. Elevated concentrations of N may be toxic to rooted macrophytes and may inhibit growth, supporting the observation by Carbiener *et al.* (1990) that ammonium-toxicity can cause shifts in macrophyte community associations. Both open-water P and N concentrations and macrophyte biomass were higher in rivers than in lakes, possibly because rivers are the dominant receivers of nutrient-rich wastes and because flowing water decreases boundary layers at the plant surface allowing increased gas exchange and increased rates of photosynthesis (Madsen and Adams 1988; Westlake 1967). Furthermore, the higher biomass observed in rivers on a global scale may reflect a sampling bias, namely that macrophytes are often studied because they cause problems that are generally associated with rivers (such as impeding boat traffic or increasing the potential for flooding), rather than for their ecological importance as providers of habitat for fish and invertebrates and contributors to the cycling of nutrients and organic matter. A comparison to other empirical models revealed that as the complexity of aquatic plants increases from phytoplankton to periphyton and macrophytes, the predictability of biomass based on open-water P and N decreases, pointing to the importance of more than one factor in regulating abundance of higher vegetation

On a local scale, macrophytes growing in the South Saskatchewan River, SK, grew abundantly downstream of the Saskatoon sewage treatment plant, but the link between P and N concentrations and plant biomass was not clear based on *in situ* observations (Chapter 3). For example, sediment P concentrations explained only 28% of the variability in macrophyte biomass collected in 1992, and surveys of the river in 1988 demonstrated that the site of peak biomass did not correspond to the site of peak sediment and open-water nutrient concentrations. This pattern of increased growth downstream of nutrient-rich effluents was observed in the Tees River, England (Butcher 1933), the Great Stour River, England (Fox *et al.* 1989) and the Bow River, Alberta (Chambers *et al.* 1991). Artificial stream experiments employed to elucidate the relationship between sediment P and N concentrations and macrophyte growth in the South Saskatchewan River supported *in situ* observations that plant growth was P-limited. Moreover, these studies found that maximum growth was likely to occur when sediment P concentrations were greater than 200 µg/g exchangeable P. This critical concentration represents the physiological optimum of rooted macrophytes under controlled conditions. Other factors such as light availability, open-water N concentrations, and discharge rates will also affect macrophyte biomass *in situ* (Wong and Clark 1976), resulting in an ecological optimum for plant growth that may not coincide with sites where sediment P concentrations are optimal. In this study, macrophyte biomass in the South Saskatchewan River was not maximal throughout the zone of physiologically optimal sediment P concentrations, supporting the hypothesis that other factors control plant growth *in situ*.

Management strategies aimed at controlling phytoplankton production through reductions in nutrient-loading in lakes have been successful, primarily because of the strong relationship between phytoplankton biomass and open-water P and N concentrations. However, results from this study have demonstrated that while macrophyte biomass is related to open-water P and N concentrations worldwide, the predictability of this relationship is low (Chapter 2). Furthermore, macrophytes were limited by sediment P-availability in the South Saskatchewan River, SK, but sediment P and N concentrations did not explain a large amount of the variability in macrophyte biomass based on *in situ* observations (Chapter 3). Thus, while reductions in nutrient-loading to freshwater systems may result in decreased biomass of rooted macrophytes, the magnitude of this decrease cannot be quantified. Currently, agencies from across North America are setting guidelines to regulate primary production in terms of the plants themselves, rather than on water quality criteria (*e.g.* Nordin 1985; Health and Welfare Canada 1992; Saskatchewan Environment 1988; Ministère de l'Environnement du Québec 1992; U.S. EPA 1988*a* and 1988*b*), and it is recommended that plant management strategies in the South Saskatchewan River follow a similar approach. Reductions in P and N loading in the City of Saskatoon sewage effluent should be encouraged to promote long-term reductions in macrophyte abundance, while short-term management strategies should attempt to identify levels of biomass and percent cover that are considered undesirable and harvesting of the plants when necessary should be performed to maintain macrophyte abundance below these levels.

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Appendix A: Data from literature survey

A.0 LEGEND TO TABLE A1

Site	Site of waterbody investigated;
L/R	Indicates type of waterbody investigated (L = lake; R = river);
Meanbio	Mean macrophyte biomass, during period of peak biomass, in g/m^2;
Maxbio	Maximum macrophyte biomass, during period of peak biomass, in g/m^2;
TP	Total phosphorus concentration in the open-water, in μg/L;
TDP	Total dissolved phosphorus concentration in the open-water, in μg/L;
SRP	Soluble reactive phosphorus concentration in the open-water, in μg/L;
TN	Total nitrogen concentration in the open-water, in μg/L;
TKN	Total Kjeldahl nitrogen concentration in the open-water, in μg/L;
TIN	Total inorganic nitrogen concentartion in the open-water, in μg/L;
NH4	Ammonia concentration in the open-water, in μg/L;
NO2+NO3	Nitrite plus nitrate concentration in the open-water, in μg/L;
References	Data source.

Table A1: Data from literature survey

Site	L/R	Meanbio (g/m2)	Maxbio (g/m2)	TP (µg/L)	TDP (µg/L)	SRP (µg/L)	TN (µg/L)	TKN (µg/L)	TIN (µg/L)	NH4 (µg/L)	NO2+NO3 (µg/L)	References
Sheerness Cooling Pond, AB	L	208	925	120			560					Barton et al. 1991
Melton Hill Reservoir, Tenn	L	243	497	30			1195		612	40	572	Brenkert & Amundsen 1982
Stella LK, FL	L	377	458	12			460					Canfield et al. 1983
Baldwin LK, FL	L	156		11								Canfield et al. 1983
Okahumpka LK, FL	L	801	990	16			880					Canfield et al. 1983
Down Lake, FL	L	77	93	9			310					Canfield et al. 1983
Fairview LK, FL	L	617	759	10			450					Canfield et al. 1983, Canfield and Duarte 1988
Lochloosa LK, FL	L	330	411	25			1200					Canfield et al. 1983
Kerr LK, FL	L	5	7	8			220					Canfield et al. 1983
Crooked, AB	L	112	582	85	39		534		320	239	81	Chambers unpublished
Baptiste South, AB	L	81	152	138	117		546		288	198	90	Chambers unpublished
Halfmoon North, AB	L	138	307	85	22		430		202	198	4	Chambers unpublished
Lofty LK, AB	L	79.5	259	128	71		431		390	385	5	Chambers unpublished
Jenkins LK, AB	L	81.5	284	128	50		450		317	298	19	Chambers unpublished
LaDue Reservoir, Ohio	L	154	239	42								Cooke et al. 1990
Bay of Quinte, LK ON	L	33.8	145	36			670					Crowder & Bristow 1986, Robinson 1986
LK Opinicon, ON	L	310	1441	19				405				Crowder et al. 1977
Ludger, QC	L	40	208	12								Cyr & Downing 1988
Quenouilles, QC	L	182	398	10								Cyr & Downing 1988
Fournelle, QC	L	256	488	8								Cyr & Downing 1988
Champlain, QC	L	182	630	22								Cyr & Downing 1988
Brome, QC	L	9	43	16								Cyr & Downing 1988
George, QC	L	11.4	28.1	8								Duarte & Kalff 1990
Boivin, QC	L	30	62.6	125								Duarte & Kalff 1990
Little Brompton, QC	L	2.3	25.3	6								Duarte & Kalff 1990
Brompton, QC	L	0.2	0.6	3								Duarte & Kalff 1990
Montjoie, QC	L	0.1	0.3	8								Duarte & Kalff 1990
Missisquoi Bay, QC	L	9	17.7	65								Duarte & Kalff 1990
Stukely, QC	L	1	2.8	3								Duarte & Kalff 1990
Silver, QC	L	4.5	12.3	8								Duarte & Kalff 1990
Selby, QC	L	111.3	125.4	11								Duarte & Kalff 1990
Hertel, QC	L	50.4	99.8	10								Duarte & Kalff 1990
Trousers, QC	L	0.8	2.4	7								Duarte & Kalff 1990
Roxton Pond, QC	L	60.6	77.4	18								Duarte & Kalff 1990
Bowker, QC	L	1	3.3	10								Duarte & Kalff 1990
Conneley, QC	L	11.6	29.2	9								Duarte & Kalff 1990
Cromwell, QC	L	5	16.7	11								Duarte & Kalff 1990
Lovering, QC	L	4	8.4	16								Duarte & Kalff 1990
LK St. Clair, ON	L	58	58	9			478	180			298	Edwards et al. 1989
Waskesiu LK, SK	L	58	378	13.6								Evans et al. 1993
East Graham LK, Mich	L	125	125	14		5	444		17	3	14	Hough et al. 1989
Shoe LK, Mich	L	31	31	25		8	458		53	28	25	Hough et al. 1989

Table A1: Data from literature survey

Site	L/R	Meanbio (g/m2)	Maxbio (g/m2)	TP (µg/L)	TDP (µg/L)	SRP (µg/L)	TN (µg/L)	TKN (µg/L)	TIN (µg/L)	NH4 (µg/L)	NO2+NO3 (µg/L)	References
Swartvlei L, Africa	L		1950	27	15	2	462		167		28	Howard-Williams & Liptrot 1980
Loch Leven, Scotland	L	30	30	169		20	1704		1162		950	Jupp & Spence 1977
d'Argent, QC	L	34	84	13								Lalonde & Downing 1992
Memphremagog, QC	L	70	172	18								Lalonde & Downing 1992
Waterloo, QC	L	105	419	73								Lalonde & Downing 1992
Massawippi, QC	L	215	457	24								Lalonde & Downing 1992
Magog, QC	L	149	273	58								Lalonde & Downing 1992
des Iles, QC	L	36	106	6								Lalonde & Downing 1992
Orford, QC	L	61	129	7								Lalonde & Downing 1992
Echo, QC	L	521	1271	13								Lalonde & Downing 1992
Chautauqua LK, NY	L	158	200	66		29	787		427		269	Nilcholson 1981
LK Katchewanooka, ON	L	43	120	30			564	530	74	40	34	Ontario MOE & MNR 1976
Pigeon LK, ON	L	237	470	26			679	620	94	35	59	Ontario MOE & MNR 1976
Balsam LK, ON	L	90		16			363	320	63	20	43	Ontario MOE & MNR 1976
Chemung LK, ON	L	340	500	23			594	550	104	60	44	Ontario MOE & MNR 1976, MOE & MNR 1977
Rice LK, ON	L	149	409	56			753	730	83	60	23	Ontario MOE & MNR 1976
Wobel LK, Poland	L	4.8								20		Ozimek et al. 1986
Mikolajskie LK, Poland	L	35		571		490	546		630	540	90	Ozimek et al. 1986, Ozimek 1978
Sniardwy LK, Poland	L	274.8								25		Ozimek et al. 1986
Talty LK, Poland	L	110.4								146		Ozimek et al. 1986
Beldany LK, Poland	L	27.6					449		216	198	18	Ozimek et al. 1986
Maly Dubovec fishpond, Czech	L	450	450	141		97.6	1630		197	131	66.1	Pokomy et al 1984
Figure Eight LK, AB	L	547	979	60			1500					Prepas & Murphy 1987
LK Kalgaard, Denmark	L	223		44		8.5	514		106	40	66	Sand-Jensen & Sondergaard 1979
Neusiedlersee, Austria	L	10	12	50	39	14	1285	1100	336		185	Schiemer & Posser 1976, Neuhuber et al. 1979
LK Rotorua, NZ	L	265	265	41	9	4.4	202		14.3	4.5	9.8	Schwarz et al. 1993
LK Taupo, NZ	L	424	424	36	1	1.4	82.8		11.8	4.5	7.3	Schwarz et al. 1993
Econlochatchee, FL	R	2	50	100			1500					Canfield & Hoyer 1988 (report)
Reedy, FL	R	5	80	240			1800					Canfield & Hoyer 1988 (report)
Hogtown, FL	R	30	370	500			560					Canfield & Hoyer 1988 (report)
Santa Fe, FL	R	10	120	240			930					Canfield & Hoyer 1988 (report)
Hillsborough, FL	R	370	3500	290			830					Canfield & Hoyer 1988 (report)
Mills, FL	R	30	160	610			1400					Canfield & Hoyer 1988 (report)
St. Marks, FL	R	390	1200	30			360					Canfield & Hoyer 1988 (report)
Alexander Springs, FL	R	530	1600	40			410					Canfield & Hoyer 1988 + 88 report
Little Wekiva, FL	R	330	1800	600			2700					Canfield & Hoyer 1988 + 88 report
Alligator Creek, FL	R	60	560	380			820					Canfield & Hoyer 1988 + 88 report
Ichetucknee Springs, FL	R	470	1500	50			260					Canfield & Hoyer 1988 + 88 report
Wekiva, FL	R	260	1000	210			880					Canfield & Hoyer 1988 + 88 report
Wacissa, FL	R	1100	2300	40			200					Canfield & Hoyer 1988 + 88 report
Little Econlockhatchee,FL	R	10	210	230			2600					Canfield & Hoyer 1988 + 88 report
Rock Springs, FL	R	390	1300	80			1250					Canfield & Hoyer 1988 + 88 report

Table A1: Data from literature survey

Site	L/R	Meanbio (g/m2)	Maxbio (g/m2)	TP (µg/L)	TDP (µg/L)	SRP (µg/L)	TN (µg/L)	TKN (µg/L)	TIN (µg/L)	NH4 (µg/L)	NO2+NO3 (µg/L)	References
Alafia, FL	R	20	310	1950			1310					Canfield & Hoyer 1988 + 88 report
South Saskatchewan River, SK	R	232	431	76	63	44	425	359	127	61	66	Carr, Chapter 3
Bow River, AB	R	908	1788	208	172		2314	1520	1288	494	794	Chambers et al. 1991
Highwood R., AB	R	71	339	16	11		302	296	13.6	7.2	6.4	Chambers unpublished
Bere Stream, UK	R	473	544	1800			6311		4856		4370	Dawson 1976
Rainbow, FL	R	890		30			420					Duarte & Canfield 1990
Weeki Wachee, FL	R	1837		8			240					Duarte & Canfield 1990
Poe, FL	R	710		86			410					Duarte & Canfield 1990
Fannin, FL	R	1573		58			1900					Duarte & Canfield 1990
Big Blue, FL	R	1480		51			220					Duarte & Canfield 1990
Silver, FL	R	701		44			700					Duarte & Canfield 1990
Sanlando, FL	R	150		187			590					Duarte & Canfield 1990
Silver Glenn, FL	R	1693		24			20					Duarte & Canfield 1990
Rainbow 2, FL	R	2060		35			690					Duarte & Canfield 1990
Blue, FL	R	345		34			1000					Duarte & Canfield 1990
Salt, FL	R	780		22			280					Duarte & Canfield 1990
Manatee ,FL	R	1143		17			700					Duarte & Canfield 1990
Palm, FL	R	1		140			370					Duarte & Canfield 1990
Blue, FL	R	172		76			340					Duarte & Canfield 1990
Crab Tree, FL	R	553		18			460					Duarte & Canfield 1990
Dogwood, FL	R	108		37			370					Duarte & Canfield 1990
Ginnie, FL	R	720		32			530					Duarte & Canfield 1990
Detroit R.	R	174	174	9.4			435	170	423		265	Edwards et al. 1989
St. Lawrence R.	R	111	140	13.2			488	232	413		256	Edwards et al. 1989
St. Clair R.	R	164	164	5.5			498	188	471		310	Edwards et al. 1989
St. Mary's River	R	44	88	3.6			401	99	463		302	Edwards et al. 1989
Mouse Water R, UK	R	250		67		30	15781		12449		11400	Fox & Murphy 1990
Coln R, UK	R	190		111		70	32753		26057		24000	Fox & Murphy 1990
Windrush R, UK	R	340		166		120	48513		38693		35700	Fox & Murphy 1990
Petteril R, UK	R	180		254		200	14164		11153		10200	Fox & Murphy 1990
Nechako R., BC	R	119	1262	27	7	3	244	224	26	6	20	French 1995, French & Chambers 1993
San Marcos River, Texas	R	232	638	349		287	2025		1233	45	1188	Hannan & Dorris 1970
Gryde, Vestergard, SW	R	210	210	106		65	1637		1109		900	Kern-Hansen & Dawson 1978
Tvis, Sonderbaekhus, SW	R	200	200	78		40	2445		1757		1500	Kern-Hansen & Dawson 1978
Vorgod, Timring, SW	R	220	220	199		150	3321		2459		2150	Kern-Hansen & Dawson 1978
Lille, Fuglsang, SW	R	175	175	100		60	1502		1001		800	Kern-Hansen & Dawson 1978
Idom, Idom Kirkeby, SW	R	450	450	78		40	2041		1433		1200	Kern-Hansen & Dawson 1978
Haller, Sangildgard, SW	R	325	325	62		25	2849		2081		1800	Kern-Hansen & Dawson 1978
Gryde, Simonstrup, SW	R	150	150	62		25	1772		1217		1000	Kern-Hansen & Dawson 1978
Gjem, Sminge, SW	R	275	275	305		247	2984		2189		1900	Kern-Hansen & Dawson 1978
Fjederholt, Isenvad SW	R	475	475	100		60	4870		3701		3300	Kern-Hansen & Dawson 1978
Granslev, Vrangstrup, SW	R	750	750	95		55	1906		1325		1100	Kern-Hansen & Dawson 1978

Table A1: Data from literature survey

Site	L/R	Meanbio (g/m2)	Maxbio (g/m2)	TP (µg/L)	TDP (µg/L)	SRP (µg/L)	TN (µg/L)	TKN (µg/L)	TIN (µg/L)	NH4 (µg/L)	NO2+NO3 (µg/L)	References
Granslev Pot Molle, SW	R	95	95	89		50	1502		1001		800	Kern-Hansen & Dawson 1978
Lille, Ornhoj, SW	R	80	80	50		14	2176		1541		1300	Kern-Hansen & Dawson 1978
Idom, Burlund, SW	R	440	440	144		100	3388		2513		2200	Kern-Hansen & Dawson 1978
Portage Creek, Mich	R	21.1	34.4	128		85.8	1070		906	427	479	Kullberg 1974
Ashippun R., WI	R	112	273	117		41		1090	1060			Mace et al. 1984
Cedar Creek, WI	R	161	246	50		29		500	710			Mace et al. 1984
Bark R., WI	R	163	530	107		81		738	798			Mace et al. 1984
Mount Vernon Creek, WI	R	365.5	869	50		37		200	4280			Mace et al. 1984
Black Earth Creek, WI	R	282.1	617	107		52		430	2150			Mace et al. 1984
Scuppernong R., WI	R	262.6	515	27		9		830	830			Mace et al. 1984
Milwaukee R., WI	R	261	957	267		223		1235	445			Mace et al. 1984
Fox River , WI	R	147	268	147		78		1100	620			Mace et al. 1984
Mukwonago R., WI	R	57.8	116	13		2		570	30			Mace et al. 1984
Sugar Creek, WI	R	143	284	113		42		795	2375			Mace et al. 1984
Pewaukee R., WI	R	213.8	531	140		74		1050	480			Mace et al. 1984
Badfish Ck, WI	R	620	712	600		600	1400					Madsen & Adams 1988
R. Ivel, UK	R	99	183	56		20	11026		8020	150	7870	Owens & Edwards 1961
Holston R. TX	R	344	344	90		51			170			Peltier & Welch 1969
Little Conesus Ck, NY	R	387	387	303	290	234	2415		1538	60	1478	Peverly 1979
Oak Orchard Ck, NY	R	600	600	348		286	910		450	90	360	Peverly 1985
Susa R, Denmark	R	125	256	385		320	9382				6650	Sand-Jensen et al. 1989
Zschopau, Germany	R	211	1470	152		107						Werner & Weise 1982
Upper Spring Creek, Penns.	R	75.7	75.7	17	8	4	3410	440	3020	50	2970	Wright & McDonnell 1986
Slab Cabin Run, Penns.	R	381	381	1340	1350	1150	7550	2670	6720	1840	4880	Wright & McDonnell 1986
	mean	275	448	127	142	113	2407	661	2375	180	2354	
	min	0.1	0.3	3	1	1.4	20	99	11.8	3	4	
	max	2060	3500	1950	1350	1150	48513	2670	38693	1840	35700	
	n	149	121	146	16	52	101	29	68	33	58	

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Appendix B: Artificial stream pilot experiments

B.0 INTRODUCTION

To test the hypothesis that macrophyte production in lotic systems is related to sediment phosphorus (P) and nitrogen (N) concentrations, I wanted to develop growth curves for aquatic plants growing in a range of sediment nutrient concentrations. Pilot experiments were conducted to: (1) identify a rooting medium low in exchangeable P and N but which otherwise mimicked sediments in the South Saskatchewan River downstream of the Saskatoon sewage treatment facility, (2) determine the most efficient method for enriching the sediments with N-only and P-only fertilizers, (3) determine target concentrations for sediment enrichment, and (4) determine the extent to which P and N in the sediments diffuse into the overlying water.

B.1 PILOT EXPERIMENT 1: Identification of Sediment Source

The design of the artificial stream experiments necessitated that sediments low in exchangeable P and N be used so that they could be enriched at a range of concentrations spanning natural riverbed nutrient levels. Sediment-bound P and N in the South Saskatchewan River range from 28 to 360 μg/g exchangeable P and <1 to 116 μg/g exchangeable N (Chambers and Prepas 1994) and it was desirable that background nutrient concentrations of sediments in the artificial stream experiments were at or near the lowest recorded values. Sediments in prairie rivers tend to be spatially heterogeneous both in terms of nutrient availability and particle size whereas terrestrial soils are more homogeneously distributed, relatively easy to collect, and can mimic river sediments in terms of fertility. Thus, to reduce collection times and ensure that relatively homogeneous samples were collected, terrestrial soils were used in place of river sediments as rooting media in the artificial stream experiments.

Two terrestrial soil types were investigated as possible rooting media for the plants in the artificial stream experiments: (1) C horizon (approximately 50 cm below surface) soils of the Bradwell association (described by Tiessen et al. 1982), and (2) roadside soils collected near the town of Asquith, SK. Both types of soil were analysed for sediment exchangeable P and N concentrations (analytical methods described in Chapter 3) and particle size distribution (following McKeague 1978). The Bradwell and Asquith soils had exchangeable N concentrations that were comparable to the lowest concentrations found in river sediments (Table B1). Exchangeable P concentrations, however, were higher than river sediments, and the soils were therefore diluted with pure silica sand (≈ 2.5 µg/g exchangeable P) to lower sediment P levels. A dilution of one part Bradwell soil to four parts silica sand was required to obtain P concentrations which approached the targeted 30 µg/g exchangeable P concentration (Figure B1). Asquith soils had lower exchangeable P concentrations than pure Bradwell soils prior to dilution with silica sand (Table B1) and 1:1 and 2:1 silica sand to Asquith soil dilutions produced sediment P concentrations near the targeted 30 µg/g exchangeable P, in 1994 and 1995, respectively (Figure B1). Particle size analysis revealed that Asquith soils most closely resembled South Saskatchewan River sediments (Table B2), and it was therefore decided that Asquith soils, diluted 1:1 with silica sand in the 1994 experiments, and 2:1 with silica sand in the 1995 experiments, would be used as the rooting media in the artificial stream experiments.

B.2 PILOT EXPERIMENT 2: Determination of Enrichment Method

Three enrichment methods were compared to unenriched sediments (control) to determine the most efficient way to increase sediment nutrient concentrations: (1) fertilizer mixed into sediments (mixed), (2) fertilizer packaged in nylon bags and buried in sediments (bag), and (3) fertilizer placed at the bottom of pots and allowed to diffuse throughout the sediments (bottom). Sediments were enriched with either P-only or N-only fertilizers. Westco ammonium-nitrate fertilizer (34.5-0-0) was used as a N source for the sediments and Vigoro "Super Triple Phosphate" (0-46-0) was used as a P source. Enrichment methods were tested at low and high N and P doses, such that 785 mL of

Table B1: Nutrient concentrations of Bradwell and Asquith soils

Soil Type	Exchangeable P (μg/g DW)	Exchangeable N (μg/g DW)
Bradwell soil	118	< 1
Asquith soil 1994	73	< 1
Asquith soil 1995	110	< 1

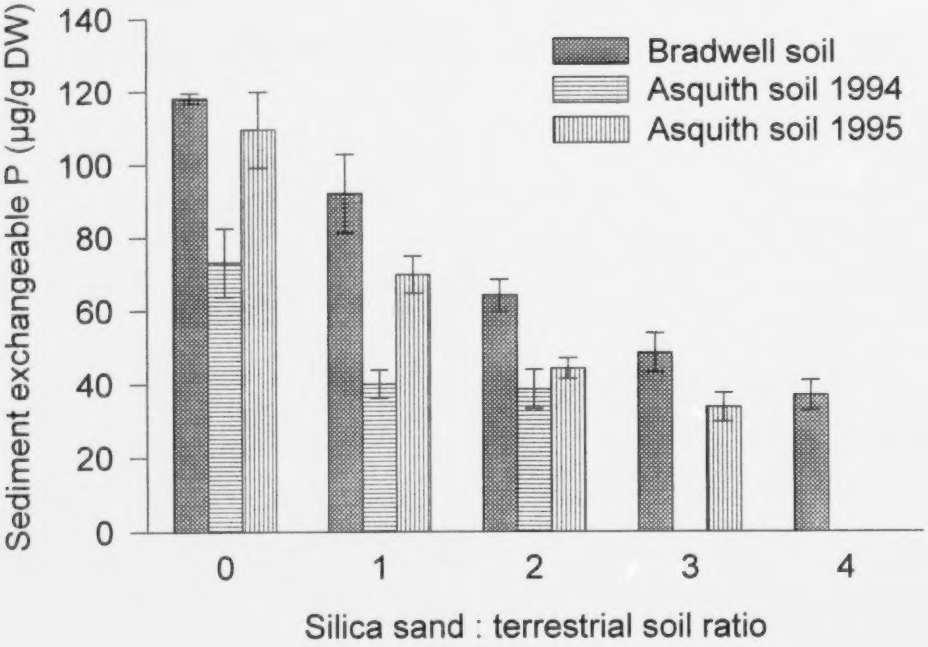

Figure B1: Sediment exchangeable P concentrations of pure soils and soils diluted with silica sand to lower sediment P levels. Data are mean ± 1 SE.

Table B2: Particle size distribution - Potential sediments

Sediment Type	Sand (%)	Silt (%)	Clay (%)
South Saskatchewan River sediment	76	10	14
Bradwell soil	30	47	23
Asquith soil	90	3	7
Pure silica sand (sieve analysis only)	100	0	0

sediment were enriched with 2 g of fertilizer for the Low N and P treatments and 8 g of fertilizer for the High N and P treatments.

Sediments used in this experiment were undiluted Bradwell soils, as an appropriate soil low in P had not yet been identified. It was assumed that the response of sediments to the different enrichment methods would be similar, regardless of initial nutrient concentrations. Sediments were well-mixed prior to nutrient-enrichment. Enriched sediments were firmly packed in plastic pots approximately 10 cm high and 10 cm in diameter (approximately 785 mL). Each enrichment method was replicated three times per treatment and three unenriched control pots were analysed for each group of treatment doses, with a total of twelve pots per treatment. The pots were placed in one of four plastic containers, filled with distilled deionized water (DDW), according to their treatment. After five days, the pots were removed and the sediments analysed for exchangeable N and P.

The three enrichment methods were compared for each treatment dose, and tested for homogeneity of variance using the Bartlett-Box *F* test (SPSS 1993). With the exception of exchangeable P concentrations for the High P treatment, the variances for exchangeable P and N concentrations did not significantly differ from each other for each treatment type ($P > 0.05$). Mean exchangeable P concentrations in both the Low and High P treatments varied significantly with enrichment method (ANOVA, $F_{2,19} = 9.02$, $P = 0.02$ and $F_{2,19} = 5.20$, $P = 0.05$, respectively) and in both cases the method of mixing the fertilizer into the sediments resulted in the highest P concentrations (Figure B2). Mean exchangeable N in the Low N treatment also varied significantly with enrichment method (ANOVA, $F_{2,19} = 44.0$, $P < 0.001$), with the mixed method resulting in the highest concentration (Figure B2). Enrichment methods for the High N treatment did not significantly differ from each other (ANOVA, $F_{2,19} = 0.24$, $P = 0.80$) (Figure B2). Unexpectedly, P concentrations in the Low and High N treatments also varied significantly from each other (ANOVA, $F_{3,24} = 11.8$, $P = 0.002$ and $F_{3,24} = 17.8$, $P =$

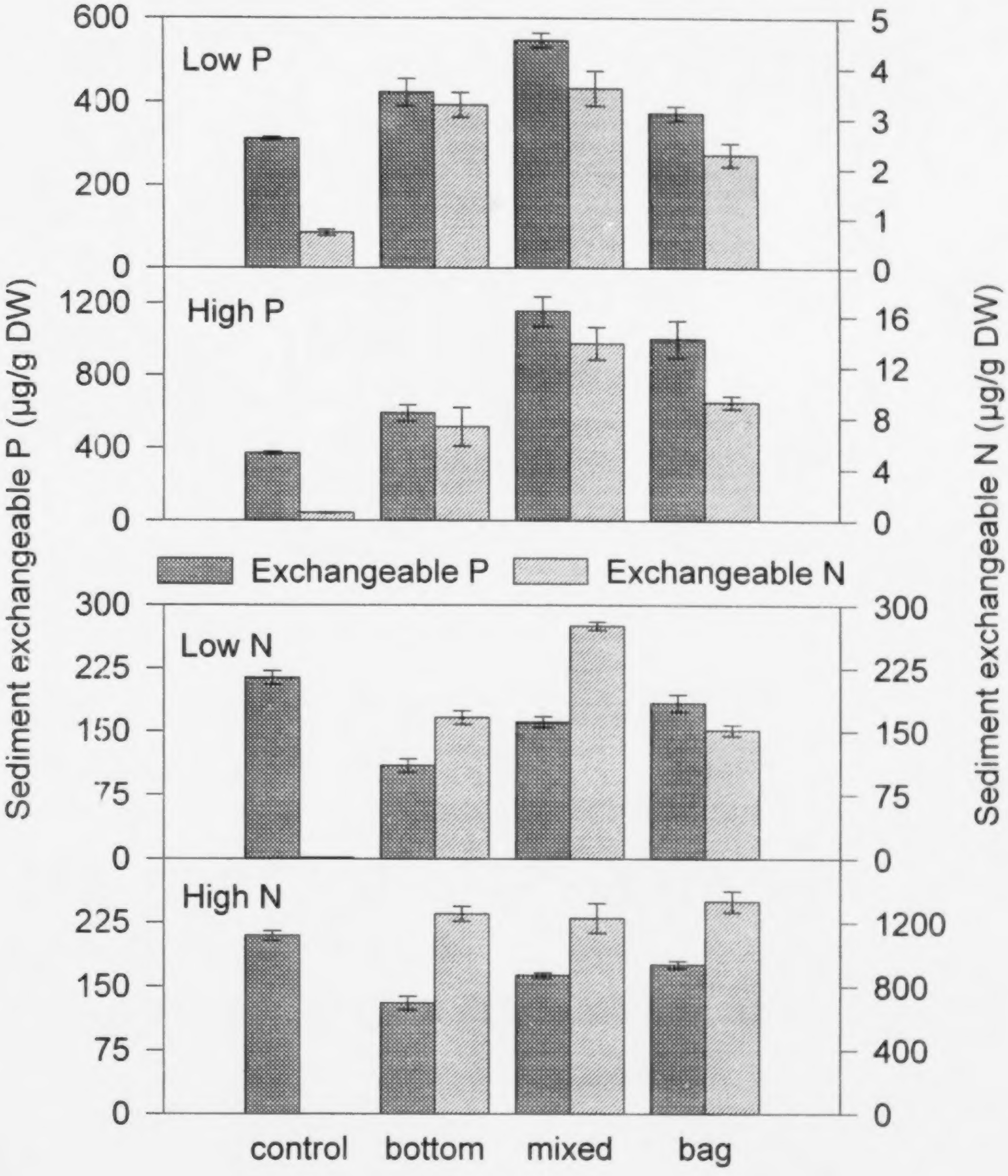

Figure B2: Exchangeable P (left bars) and N (right bars) concentrations of control and enriched (bottom, mixed, bag) sediments in Low and High P and N experiments. Data are mean ± 1 SE.

0.001, respectively) (Figure B2). It was assumed that these variations were due to background variability in the P content of the soils. These results showed that the method of mixing fertilizer into the sediments resulted in the highest nutrient enrichment and it was decided that this method would therefore be used in the artificial stream experiment.

Further analysis of the sediments in this preliminary experiment revealed that the addition of P-only fertilizer resulted in an increase in exchangeable N concentrations such that all three enrichment methods for both Low and High P treatments had higher N concentrations than the control pots (Figure B2). Exchangeable N concentrations did not significantly differ between the three enrichment methods for either the Low or High P treatments (Tukey multiple comparison tests; $0.2 < P < 0.5$, $0.1 < P < 0.2$, respectively), but controls varied significantly from the bottom and mixed methods in the Low P treatment ($0.025 < P < 0.05$) and from the mixed methods in the High P treatment ($0.001 < P < 0.005$) (Figure B2). When P-only fertilizer dissolves in the sediments, hydrogen ions are released and these compete for adsorption sites with ammonium (NH_4^+). Hydrogen ions have the same valence but smaller surface area than NH_4^+ ions and therefore adsorb more readily to clay particles, releasing NH_4^+ ions into solution.

B.3 PILOT EXPERIMENT 3: Establishing Target Nutrient Concentrations

The desired range of sediment P concentrations for the sediments in the 1994 and 1995 artificial stream experiments was from 30 to 600 µg/g and 30 to 200 µg/g exchangeable P, respectively, as these encompass the range of concentrations reported for sediments collected in the South Saskatchewan River (Chambers and Prepas 1994). Pilot experiments were conducted in 1994 and 1995 to determine the amounts of fertilizer required to achieve these ranges.

Asquith soil mixed with one and two parts silica sand in the 1994 and 1995 target experiments, respectively, was used as the sediment source. Vigoro "Super Triple

Phosphate" (0-46-0) P-only fertilizer was used as the P-source in both experiments. Sediments were enriched at eight doses (unamended, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0 and 4.0 g fertilizer added) and three replicate pots were tested for each dose. The fertilizer was mixed thoroughly with the sediments and these were packed into experimental pots (785 mL) that were randomly distributed among four large plastic containers filled with DDW. Pots were equilibrated in their containers for five days after which sediments were analysed for exchangeable P concentrations.

Sediment exchangeable P concentrations were directly related to the amount of P-only fertilizer added to the sediments in both the 1994 and 1995 experiments ($r^2 = 0.89$, $P < 0.0001$; $r^2 = 0.97$, $P < 0.05$, respectively) (Figure B3). Based on the relationship between P-only fertilizer and sediment P concentrations (Figure B3), it was anticipated that an addition of 5 g fertilizer in 1994 would result in an exchangeable P concentration near 625 µg/g DW, and that an addition of 1.0 g P-only fertilizer in 1995 would produce a sediment exchangeable P concentration of approximately 200 µg/g DW.

B.4 PILOT EXPERIMENT 4: Determination of Nutrient Release from Sediments

To determine the extent of diffusion of N and P from enriched sediments into the overlying water and the change in sediment nutrient concentration over time, sediments enriched at one of three nutrient doses (1.0 and 3.0 g P-only fertilizer and 3.0 g ammonium-nitrate fertilizer, plus untreated controls) were firmly packed into experimental pots (27 replicate pots per treatment) and these were placed according to their treatment in large tanks filled with untreated South Saskatchewan River water. Three pots from each treatment were randomly sampled at 24 hours and 7 days following immersion in the tanks. Sediment samples were collected and frozen for later analysis of exchangeable P and exchangeable N concentrations. Water samples were collected 5 and 12 days following immersion of the sediments into the tanks and analysed for soluble reactive P (SRP).

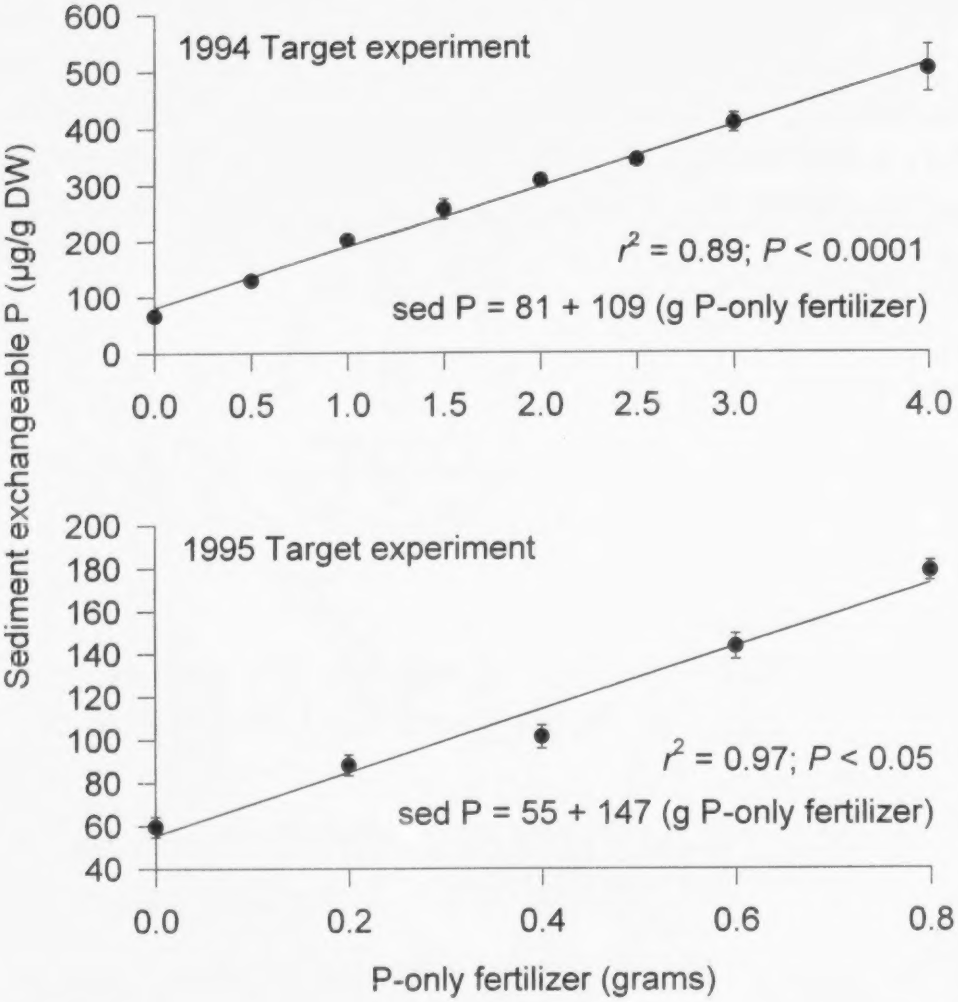

Figure B3: Relationship between exchangeable P concentrations and quantity of P-only fertilizer added to sediments in 1994 and 1995 target experiments. Data are mean ± 1 SE.

SRP concentrations in tanks with sediments enriched at 3.0 g P-only fertilizer averaged 275 μg/L compared to < 1 μg/L in the control tanks after five days, while after twelve days SRP in these tanks was greater than 550 μg/L compared to 1.7 μg/L in the controls. Based on these observations, it was evident that nutrient diffusion from the pots would occur in the artificial stream experiments and the decision was made to cover the experimental pots with plastic lids to minimize diffusion. It was also decided that additional pots would be placed in the artificial streams to be sampled several times over the course of each experiment to monitor changes in sediment nutrient concentrations.

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Appendix C: Artificial stream experimental data

C.0 LEGEND TO TABLES C1, C2, AND C3

Treatment	Treatment name refers to quantity of fertilizer added to sediments, in grams (e.g. treatment "0.5P" implies that 0.5 g of P-only fertilizer was added to the sediments in each pot);
Pot #	Reference number to identify pots, plants, and treatments;
N-only, P-only fertilizer	Weight in grams of ammonium-nitrate and P-only fertilizer added to sediments in pots;
Exchangeable N, P	Sediment N and P concentrations at the completion of the artificial stream experiments, in μg/g DW. Exchangeable N not analysed for all pots in the 1995 experiments;
Initial biomass	Initial dry weight (in grams) of macrophytes at the time of transplanting. Biomass converted to dry weight based on a fresh to dry weight ratio determined from additional plants for each experiment;
Final biomass	Oven-dry weight (in grams) of macrophytes at the completion of the artificial stream experiments;
Change in biomass	Final biomass minus initial biomass, in grams dry weight;
Tissue P, N	Macrophyte tissue nutrient concentrations at the completion of the experiments.

Table C1: P. pectinatus 1994

Treatment	Pot #	N-only fertilizer (g)	P-only fertilizer (g)	Exchangeable N (µg/g)	Exchangeable P (µg/g)	Initial Biomass (g DW)	Final Biomass (g DW)	Change in Biomass (g DW)	Tissue P (mg/g)	Tissue N (mg/g)
0N0P	1	0.00	0.00	0.51	44.13	0.16	0.03	-0.13		
0N0P	2	0.00	0.00	0.51	46.71	0.08	0.05	-0.03		
0N0P	3	0.00	0.00	0.46	39.35	0.22	0.21	-0.01	2.66	23.87
0N0P	4	0.00	0.00	0.39	41.99	0.14	0.33	0.19	2.24	18.70
0N0P	5	0.00	0.00	0.40	47.80	0.08	0.02	-0.06		
0N0P	6	0.00	0.00	0.27	47.17	0.14	0.09	-0.05	1.85	15.42
0N0P	7	0.00	0.00	0.49	48.60	0.12	0.14	0.03	2.62	28.27
0N0P	8	0.00	0.00	0.36	52.23	0.21	0.19	-0.02	1.89	20.59
0P	121	2.50	0.00	205.00	37.58	0.16	0.09	-0.07		
0P	122	2.51	0.00	188.90	36.80	0.18	0.22	0.04	1.97	24.14
0P	123	2.50	0.00	194.65	41.66	0.13	0.08	-0.06	2.73	33.31
0P	124	2.51	0.00	167.03	37.16	0.08	0.07	-0.01	3.96	34.35
0P	125	2.51	0.00	198.16	45.56	0.15	0.11	-0.04	1.85	24.57
0P	126	2.52	0.00	179.51	51.59	0.15	0.10	-0.05		
0P	127	2.51	0.00	197.87	50.48	0.24	0.33	0.09	1.03	23.21
0P	128	2.50	0.00	228.75	58.59	0.12	0.06	-0.07		
0.5P	133	2.51	0.51	154.56	124.29	0.25	0.02	-0.23		
0.5P	134	2.51	0.51	233.73	108.55	0.10	0.28	0.18	4.59	28.77
0.5P	135	2.51	0.51	239.86	181.20	0.19	0.32	0.14	6.68	32.99
0.5P	136	2.51	0.51	194.95	89.53	0.14	0.21	0.07	6.59	38.29
0.5P	137	2.51	0.51	258.05	112.26	0.12	0.10	-0.01	3.23	26.67
0.5P	138	2.52	0.51	260.16	104.51	0.11	0.14	0.03	3.22	27.83
0.5P	139	2.52	0.51	205.11	178.10	0.11	0.66	0.55	3.28	23.75
0.5P	140	2.51	0.51	228.74	140.30	0.22	0.70	0.47	4.50	30.71
1.0P	145	2.50	1.02	163.06	169.46	0.11	0.06	-0.05		
1.0P	146	2.52	1.02	138.06	204.27	0.29	0.39	0.10	5.98	30.67
1.0P	147	2.52	1.01	173.43	199.70	0.06	0.03	-0.03		
1.0P	148	2.51	1.02	223.28	201.27	0.16	0.02	-0.14		
1.0P	149	2.51	1.02	189.30	273.21	0.25	0.66	0.41	4.47	28.99
1.0P	150	2.51	1.02	191.95	97.40	0.13	0.37	0.25	5.44	31.76
1.0P	151	2.51	1.01	141.49	225.29	0.15	0.04	-0.11		
1.0P	152	2.51	1.01	203.76	268.27	0.07	0.24	0.17	5.96	29.31
1.5P	157	2.51	1.51	198.05	231.85	0.18	0.10	-0.08	1.26	16.48
1.5P	158	2.52	1.51	200.71	309.07	0.10	0.24	0.14	6.99	35.97
1.5P	159	2.52	1.52	210.37	382.98	0.16	0.20	0.04	3.76	26.91
1.5P	160	2.52	1.51	205.74	266.73	0.22	0.68	0.46	5.39	29.89
1.5P	161	2.51	1.52	197.46	270.40	0.16	0.34	0.19	5.89	26.67
1.5P	162	2.51	1.51	209.48	221.79	0.12	0.13	0.02	2.51	31.89
1.5P	163	2.51	1.51	122.93	293.46	0.16	0.46	0.30	7.12	30.95
1.5P	164	2.52	1.51	218.86	344.62	0.13	0.91	0.78	5.84	34.57
2.0P	169	2.50	2.02	221.13	399.68	0.10	0.10	-0.00	1.45	19.31

Table C1: P. pectinatus 1994

Treatment	Pot #	N-only fertilizer (g)	P-only fertilizer (g)	Exchangeable N (µg/g)	Exchangeable P (µg/g)	Initial Biomass (g DW)	Final Biomass (g DW)	Change in Biomass (g DW)	Tissue P (mg/g)	Tissue N (mg/g)
2.0P	170	2.52	2.02	182.11	340.52	0.11	0.09	-0.02	3.89	24.60
2.0P	171	2.51	2.01	224.43	544.78	0.07	0.22	0.16	7.79	33.71
2.0P	172	2.51	2.02	176.27	299.03	0.18	0.48	0.30	6.71	30.60
2.0P	173	2.51	2.01	247.10	431.35	0.11	0.02	-0.08		
2.0P	174	2.50	2.01	202.92	443.66	0.13	0.29	0.16	6.04	28.51
2.0P	175	2.52	2.00	181.12	400.41	0.12	0.34	0.22	6.32	29.55
2.0P	176	2.50	2.02	214.01	401.34	0.26	0.78	0.52	5.86	27.80
2.5P	181	2.51	2.52	168.73	458.82	0.15	0.42	0.27	6.65	32.03
2.5P	182	2.51	2.52	149.81	396.56	0.15	0.34	0.18	6.04	32.47
2.5P	183	2.52	2.50	181.76	413.93	0.19	0.59	0.40	6.02	31.42
2.5P	184	2.51	2.52	179.59	477.55	0.07	0.19	0.12	8.10	37.10
2.5P	185	2.52	2.51	210.18	572.57	0.12	0.24	0.12	4.40	27.04
2.5P	186	2.50	2.52	204.61	605.46	0.08	0.16	0.08	8.04	37.54
2.5P	187	2.51	2.52	189.51	475.62	0.08	0.07	-0.02		
2.5P	188	2.52	2.51	177.49	383.11	0.14	0.38	0.24	6.04	33.57
3.0P	193	2.51	3.02	279.42	645.20	0.22	0.21	-0.01	6.78	27.70
3.0P	194	2.51	3.00	270.43	705.99	0.14	0.12	-0.02	3.56	27.06
3.0P	195	2.52	3.01	242.01	619.32	0.11	0.73	0.62	5.42	29.03
3.0P	196	2.53	3.02	275.07	767.51	0.17	0.58	0.41	6.76	32.42
3.0P	197	2.51	3.01	258.04	573.54	0.11	0.09	-0.02		
3.0P	198	2.51	3.01	250.20	772.64	0.10	0.01	-0.08		
3.0P	199	2.50	3.00	272.62	681.53	0.10	0.08	-0.02	6.61	27.03
3.0P	200	2.50	3.02	272.70	653.95	0.18	0.26	0.08	6.54	24.95
3.0P	85	2.52	3.00	183.48	526.89	0.11	0.19	0.08	8.38	40.54
3.0P	86	2.51	3.01	119.77	575.35	0.19	0.69	0.50	6.32	34.08
3.0P	87	2.51	3.02	200.58	539.30	0.12	0.32	0.20	5.31	30.38
3.0P	89	2.52	3.02	251.17	527.86	0.28	1.43	1.14	5.72	28.76
3.0P	90	2.51	3.02	356.72	858.70	0.11	0.27	0.15	6.89	33.50
3.0P	91	2.51	3.01	409.90	674.63	0.13	0.20	0.07		
3.0P	92	2.50	3.02	186.78	697.78	0.13	0.45	0.32	6.51	34.05
4.0P	205	2.50	4.03	184.73	626.02	0.16	0.69	0.53	4.62	31.64
4.0P	206	2.52	4.01	213.40	681.40	0.18	0.65	0.47	6.11	31.27
4.0P	207	2.51	4.01	167.17	817.62	0.09	0.48	0.38	7.03	29.94
4.0P	208	2.51	4.02	149.32	732.69	0.10	0.44	0.34	6.43	34.41
4.0P	209	2.50	4.01	199.18	779.80	0.28	1.07	0.79	4.37	23.10
4.0P	210	2.52	4.02	175.02	839.21	0.12	0.14	0.02	8.18	31.09
4.0P	211	2.50	4.01	178.81	1009.65	0.11	0.08	-0.03	1.72	17.31
4.0P	212	2.50	4.02	146.82	685.64	0.16	0.48	0.31	6.86	28.48
5.0P	217	2.51	5.02	172.29	599.06	0.17	0.28	0.11	6.26	33.82
5.0P	218	2.51	5.01	212.62	1064.67	0.22	1.68	1.46	5.94	30.28
5.0P	219	2.50	5.01	209.00	962.83	0.08	0.24	0.15	7.19	29.66

Table C1: P. pectinatus 1994

Treatment	Pot #	N-only fertilizer (g)	P-only fertilizer (g)	Exchangeable N (µg/g)	Exchangeable P (µg/g)	Initial Biomass (g DW)	Final Biomass (g DW)	Change in Biomass (g DW)	Tissue P (mg/g)	Tissue N (mg/g)
5.0P	220	2.52	5.01	197.86	829.04	0.12	0.41	0.29	6.92	30.68
5.0P	221	2.52	5.00	236.25	940.57	0.21	0.50	0.29	7.51	37.27
5.0P	222	2.50	5.00	206.74	910.76	0.10	0.17	0.07	5.53	23.67
5.0P	223	2.51	5.01	232.06	974.40	0.11	0.05	-0.05		
5.0P	224	2.52	5.03	214.97	1249.45	0.17	0.61	0.44	5.85	25.32

Table C2: P. pectinatus 1995

Treatment	Pot #	N-only fertilizer (g)	P-only fertilizer (g)	Exchangeable N (µg/g)	Exchangeable P (µg/g)	Initial Biomass (g DW)	Final Biomass (g DW)	Change in biomass (g DW)	Tissue P (mg/g)
0P	263	2.50	0.00		62.12	0.06	0.12	0.06	1.40
0P	265	2.51	0.00		69.56	0.03	0.07	0.04	0.82
0P	266	2.50	0.00	125.97	63.51	0.05	0.02	-0.02	1.67
0P	305	2.51	0.00		54.20	0.07	0.05	-0.02	1.82
0P	309	2.52	0.00		60.54	0.08	0.18	0.10	1.06
0P	314	2.50	0.00		57.25	0.05	0.03	-0.02	1.76
0.1P	267	2.52	0.11		81.13	0.02	0.05	0.03	3.00
0.1P	268	2.50	0.10	162.60	90.69	0.04	0.06	0.02	0.16
0.1P	269	2.51	0.10		89.78	0.05	0.20	0.14	2.25
0.1P	271	2.52	0.10	114.03	89.10	0.03	0.01	-0.02	
0.1P	295	2.53	0.10		75.06	0.13	0.04	-0.10	4.56
0.1P	301	2.51	0.10		75.40	0.04	0.09	0.05	1.04
0.2P	274	2.51	0.20	119.83	101.63	0.05	0.07	0.02	3.45
0.2P	275	2.51	0.20	154.37	116.74	0.08	0.21	0.13	1.72
0.2P	278	2.51	0.20		104.56	0.08	0.10	0.03	1.64
0.2P	317	2.50	0.20		97.45	0.10	0.25	0.15	1.89
0.2P	319	2.54	0.20		99.38	0.07	0.25	0.18	2.42
0.2P	320	2.51	0.20		107.91	0.03	0.06	0.03	1.56
0.2P	321	2.51	0.20		92.89	0.07	0.04	-0.03	2.00
0.4P	285	2.51	0.40		148.22	0.07	0.14	0.07	3.68
0.4P	286	2.50	0.40		129.59	0.04	0.03	-0.01	3.12
0.4P	287	2.51	0.40		124.29	0.10	0.09	-0.00	2.80
0.4P	289	2.50	0.40	94.03	109.98	0.04	0.02	-0.02	1.53
0.4P	333	2.52	0.40	202.07	124.21	0.09	0.25	0.15	5.05
0.4P	336	2.52	0.40		138.96	0.06	0.05	-0.01	2.28
0.4P	345	2.51	0.40		129.21	0.06	0.36	0.30	3.26
0.8P	335	2.51	0.80		214.23	0.02	0.07	0.05	2.72
0.8P	339	2.51	0.80		211.47	0.06	0.09	0.03	2.36
0.8P	341	2.50	0.81	163.80	187.80	0.12	0.21	0.09	1.48
0.8P	342	2.50	0.81		211.94	0.05	0.18	0.13	5.48
0.8P	344	2.51	0.80		222.66	0.07	0.21	0.14	4.07
0.8P	375	2.51	0.80	175.37	198.42	0.08	0.10	0.03	6.75
0.8P	377	2.52	0.80		202.76	0.06	0.06	-0.00	3.70
1.0P	350	2.51	1.01		252.42	0.03	0.07	0.03	3.05
1.0P	355	2.51	1.00		375.63	0.07	0.33	0.26	3.47
1.0P	357	2.51	1.00		287.78	0.08	0.22	0.13	2.95
1.0P	388	2.52	1.00		246.01	0.04	0.23	0.18	4.10
1.0P	394	2.51	1.00		264.48	0.05	0.02	-0.02	3.43
1.0P	395	2.51	1.00		294.05	0.04	0.08	0.04	0.85

Table C3: M. exalbescens 1995

Treatment	Pot #	N-only fertilizer (g)	P-only fertilizer (g)	Exchangeable P (µg/g)	Initial Biomass (g DW)	Final Biomass (g DW)	Change in biomass (g DW)	Tissue P (mg/g)
0P	17	2.56	0.00	71.62	0.16	0.19	0.04	0.66
0P	19	2.54	0.00	107.98	0.12	0.18	0.06	0.73
0P	20	2.52	0.00	79.03	0.06	0.29	0.23	0.55
0P	21	2.57	0.00	76.28	0.04	0.12	0.07	1.32
0P	22	2.50	0.00	92.59	0.11	0.48	0.37	0.62
0P	23	2.55	0.00	74.07	0.09	0.32	0.23	0.76
0P	24	2.55	0.00	64.40	0.06	0.11	0.06	0.40
0.1P	30	2.53	0.10	87.88	0.11	0.66	0.55	1.29
0.1P	31	2.56	0.10	83.44	0.09	0.66	0.56	1.26
0.1P	33	2.53	0.10	79.95	0.10	0.57	0.48	1.26
0.1P	34	2.53	0.10	100.04	0.05	0.23	0.18	1.01
0.1P	35	2.50	0.10	99.91	0.05	0.18	0.13	0.83
0.1P	36	2.53	0.10	111.08	0.05	0.24	0.18	0.87
0.2P	41	2.53	0.20	75.46	0.07	0.37	0.30	1.42
0.2P	43	2.50	0.20	110.70	0.13	0.85	0.72	1.96
0.2P	44	2.51	0.20	96.33	0.09	0.13	0.04	0.96
0.2P	45	2.51	0.20	116.63	0.09	0.68	0.59	1.95
0.2P	46	2.51	0.20	112.12	0.08	0.63	0.55	1.50
0.2P	47	2.54	0.20	93.77	0.07	0.42	0.36	1.58
0.2P	48	2.51	0.20	112.21	0.06	0.19	0.13	1.53
0.3P	53	2.51	0.30	113.54	0.10	0.44	0.34	1.69
0.3P	55	2.51	0.30	118.31	0.12	0.68	0.57	1.91
0.3P	57	2.52	0.31	120.63	0.11	0.43	0.32	2.34
0.3P	59	2.51	0.30	140.17	0.04	0.12	0.07	1.86
0.3P	60	2.50	0.31	123.08	0.08	0.70	0.62	2.75
0.4P	68	2.51	0.41	159.70	0.09	0.77	0.68	1.68
0.4P	69	2.53	0.40	110.94	0.06	0.39	0.33	4.12
0.4P	70	2.51	0.40	171.11	0.09	0.24	0.15	2.37
0.4P	71	2.50	0.40	168.76	0.10	0.79	0.69	3.02
0.4P	72	2.50	0.40	157.25	0.08	0.54	0.46	4.07
0.6P	79	2.50	0.60	172.29	0.10	0.08	-0.01	1.49
0.6P	80	2.52	0.61	164.88	0.05	0.51	0.46	3.00
0.6P	81	2.52	0.60	179.15	0.06	0.68	0.62	4.36
0.6P	82	2.52	0.61	164.72	0.09	0.34	0.25	2.78
0.6P	83	2.52	0.60	183.45	0.07	0.49	0.42	3.48
0.6P	84	2.51	0.60	154.56	0.11	1.06	0.95	4.80
0.8P	88	2.50	0.80	211.36	0.08	0.31	0.24	5.44
0.8P	89	2.51	0.80	224.58	0.08	0.19	0.11	3.78
0.8P	90	2.51	0.80	181.20	0.10	1.22	1.12	5.46
0.8P	91	2.50	0.80	205.88	0.12	1.51	1.39	3.93
0.8P	92	2.51	0.80	206.19	0.11	0.26	0.15	4.37

Table C3: M. exalbescens 1995

Treatment	Pot #	N-only fertilizer (g)	P-only fertilizer (g)	Exchangeable P (µg/g)	Initial Biomass (g DW)	Final Biomass (g DW)	Change in biomass (g DW)	Tissue P (mg/g)
0.8P	93	2.50	0.80	221.70	0.07	0.45	0.38	3.79
0.8P	94	2.51	0.80	217.91	0.08	0.61	0.52	3.47
0.8P	95	2.51	0.80	258.13	0.09	0.63	0.54	4.43
0.8P	96	2.51	0.80	232.10	0.07	0.29	0.22	4.97
1.0P	101	2.51	1.00	290.55	0.12	0.88	0.76	2.16
1.0P	102	2.50	1.00	314.36	0.13	0.41	0.28	3.56
1.0P	103	2.51	1.00	278.86	0.10	0.69	0.59	4.03
1.0P	104	2.51	1.00	284.82	0.07	1.13	1.05	4.76
1.0P	105	2.52	1.00	280.15	0.06	0.59	0.53	3.82
1.0P	106	2.52	1.00	247.94	0.17	2.34	2.16	3.29
1.0P	107	2.50	1.00	289.61	0.10	1.19	1.09	4.04
1.0P	108	2.51	1.00	283.60	0.09	0.67	0.58	5.01